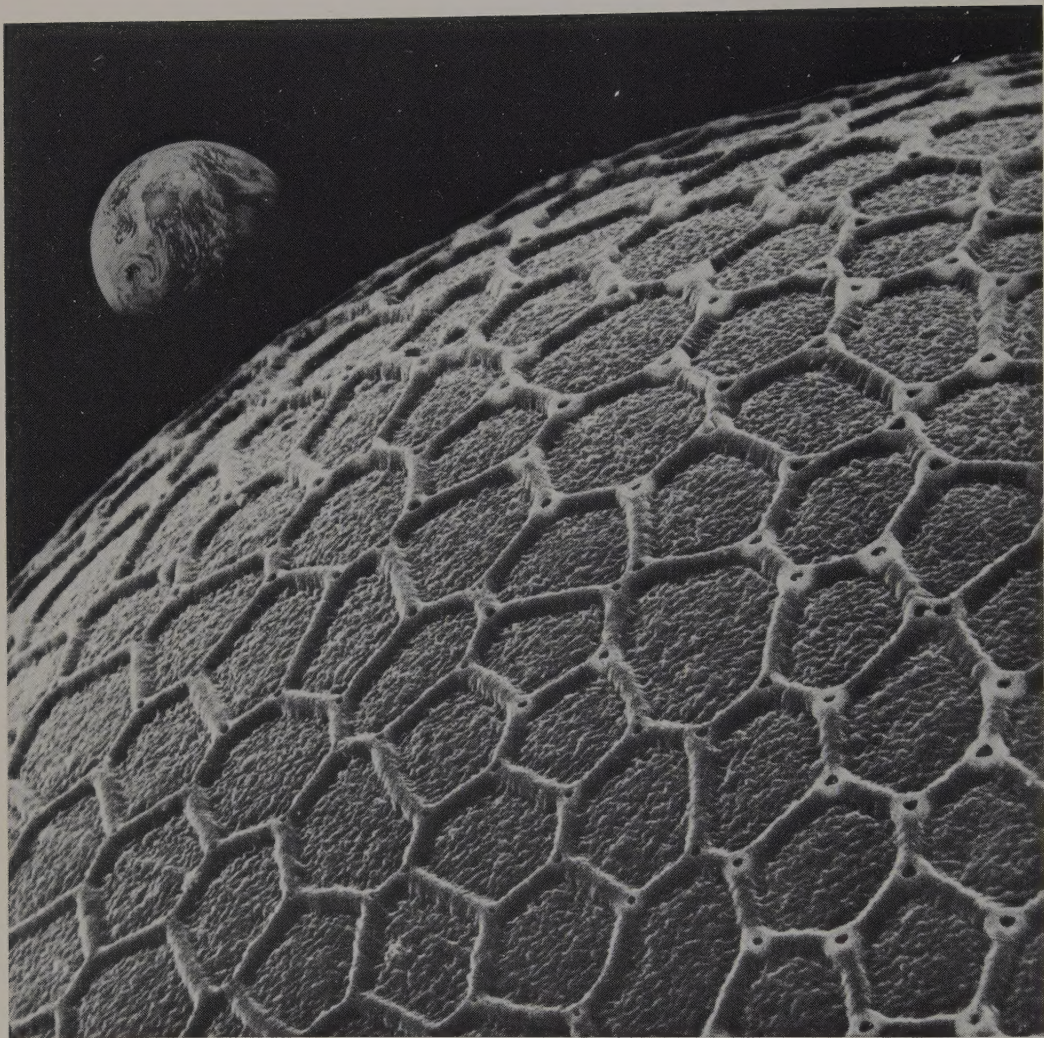


THE INSECTS
OF AUSTRALIA

SUPPLEMENT 1974



The scanning electron microscope has revolutionized study of surface detail of minute objects just as much as sophistication in rocket technology has advanced knowledge of the earth-moon system.

Egg of *Pterolocera* sp., Lepidoptera-Anthelidae, $\times 450$

The Earth, $\times \frac{1}{450,000,000}$

[Photographs by B. K. Filshie and by courtesy of NASA]

THE INSECTS OF AUSTRALIA

A Textbook for Students and Research Workers

SUPPLEMENT 1974

SPONSORED BY

THE DIVISION OF ENTOMOLOGY

COMMONWEALTH SCIENTIFIC AND

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PREFACE

It was a defect of *The Insects of Australia*, as of most large works, that it was out of date by the time it was printed. It was issued in February 1970, yet its presentation of the state of knowledge was barely adequate for 1967 and not at all for 1968. When, therefore, the time came to prepare the volume for reprinting, considerable thought was given to ways and means of overcoming this defect and others that had become evident.

After discussion with Mr P. A. Ryan, director of Melbourne University Press, it was agreed that the only practicable and economical solution was to publish a slim supplementary volume in the same format as the original. Its purpose would be to bring the general coverage of literature up to the end of 1973, or a little beyond, and at the same time to make good significant errors and omissions and record changes that had occurred, or come to notice, in taxonomic

names. It was realized, too, that some topics had been inadequately covered in the book, either from lack of space or because they have advanced notably since it was written, so it was decided to include a few special sections as well. All this had to be done in the briefest possible way, if the *Supplement* were not to defeat its own ends.

It could not, naturally, be balanced in the way that was attempted for the parent book—some chapters are very short, others relatively long—nor could the chapters themselves be subdivided in the same uniform way. Nevertheless, they follow the same sequence, and cross-references to pages and illustrations in the original text are printed in bold-face figures to distinguish them from cross-references and citations within the *Supplement*.

Our gratitude is due to nearly everyone acknowledged in the original volume, and

again especially to Mrs S. W. Bailey (then Miss Robin Holland) and Miss Josephine Cardale for their help in the preparative and subeditorial parts of the work, including the index. Miss Cardale also had the task of gathering much of the information for Dr Riek's chapters during his absence abroad. Mrs B. Rankin, Mrs S. Monteith (then Miss S. Curtis), Mrs G. C. Palmer and Mr L. A. Marshall again provided many of the illustrations, with additional blocks by Mrs A. Klinkenberg, Mr R. Kohout, Dr B. P. Moore and some of the authors. Figures 1 to 5 were drawn by Mrs Joan Goodrum of the Australian National University. Photographs by Messrs C. Lourandos, J. P. Green, D. Wilson and Dr G. C. Webb, and scanning electron micrographs by Dr B. K. Filshie, Mr C. D.

Beaton and Mr B. R. Pitkin complete the illustrations.

We are indebted also to the National Aeronautics and Space Agency of the United States for part of the frontispiece, to the Australian Academy of Science for permission to publish Figure 12, and to the editor of the *Australian Journal of Zoology* for Figure 42. The unacknowledged portions of Figures 27 to 33 are from the main volume of *The Insects of Australia*.

And finally we would record with particular pleasure that the bonds that formed between Melbourne University Press and the editorial group in the Division of Entomology during publication of *The Insects of Australia* have been strengthened by this second venture together.

D. F. WATERHOUSE

Chief,

Division of Entomology,

CSIRO

Canberra

31 January 1974

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SKELETAL ANATOMY

by I. M. MACKERRAS

There is little to add at the level at which this chapter was written. Matsuda (1965, 1970) has published detailed reviews of the comparative morphology of the head and thorax, both papers being of greater concern to the morphologist than to the general entomologist. Hamilton (1971-2) developed new ideas on the phylogeny of venational patterns in the Neoptera and also made a number of changes in the notation of wing veins. On the evidence presented, his conclusions cannot be regarded as other than tentative.

Scudder (1971) has presented an admirable review of modern work on the terminalia of both sexes, including reference to the second edition of Tuxen's *Glossary* and other

1970 publications. He has added support to the theory (p. 21) that at least the clasping organs of the male, as well as the ovipositor of the female, were derived from abdominal limbs, and further support has come from ontogenetic studies of the terminalia of mosquitoes by Voorhees and Horsfall (1971, and earlier papers in the series).^{*} Mickoleit (1973) has made a comparative study of the ovipositor in the neuropteroid orders and included a diagram (see Fig. 11) showing the homologies and relationships of the parts in the major lines of endopterygote evolution.

Other papers on anatomy will be noted in chapters to which they are more relevant.

^{*} See also Birket-Smith (1974).

GENERAL ANATOMY AND PHYSIOLOGY

Reviews have been limited to two topics in which there have been major recent advances.

INSECT VISION

by G. A. HORRIDGE

The eyes of insects are, broadly, of three kinds (p. 45): *compound eyes* occurring in larvae of apterygotes and exopterygotes and adults of almost all orders; *ocelli* (usually three) which occur in so many orders that they must have been present in ancestral insects; and *stemmata*, the temporary eyes of endopterygote larvae. Although belonging to

the Endopterygota, the larvae of Mecoptera have compound eyes with typical ommatidia (Bierbrodt, 1942) rather like those of primitive exopterygotes. Collembola, alone among the entognathous hexapods, have primitive eyes that are really separated ommatidia, each with a full complement of cell types.

How an insect uses ocelli in addition to

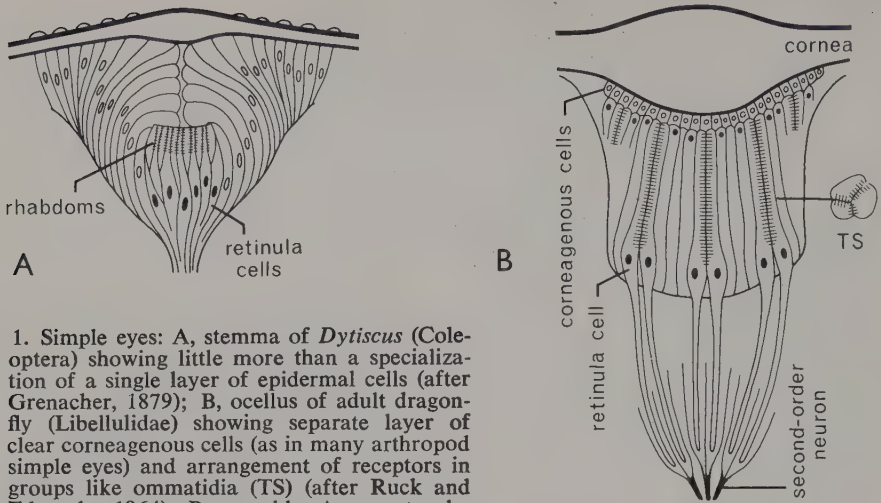


Fig. 1. Simple eyes: A, stemma of *Dytiscus* (Coleoptera) showing little more than a specialization of a single layer of epidermal cells (after Grenacher, 1879); B, ocellus of adult dragonfly (Libellulidae) showing separate layer of clear corneogenous cells (as in many arthropod simple eyes) and arrangement of receptors in groups like ommatidia (TS) (after Ruck and Edwards, 1964). Presumably A operates by having receptors in the plane of the image, but B operates by the action of the receptors as light guides. Thus the two main types of eye are exemplified even in larvae.

compound eyes is unknown. Basically, ocelli are composed of a layer of receptor cells, often with an overlying layer of clear epidermal cells beneath the cornea, all pressed together under a single corneal lens. Stemmata of many larvae of Coleoptera, Symphyta and Lepidoptera are quite similar to ocelli of some adults, e.g. Neuroptera, Lepidoptera and Hemiptera; others are simpler (Fig. 1A). The receptor cells of both are arranged in groups like ommatidia (Fig. 1B). The more highly developed stemmata have their own optic ganglia, but all disappear in the pupal stage. There is a variety of other simple larval eyes, of which there are few modern descriptions.

Compound eyes consist of reduplicated ommatidia, each of which has a remarkably constant composition of a transparent corneal lens, 4 clear cone cells, 2 principal pigment cells, several accessory pigment cells and 8 or 9 (or occasionally up to 16) modified neurons which are the photoreceptor or retinula cells. The pattern is usually a very regular array across the eye, and shows a remarkable diversity between families not obviously correlated with function. One ommatidium with its complement of these cells lies under each facet, and in some

aquatic insects, particularly in water beetles, the cornea is smooth. Each retinula cell has a specialized structure which is a parallel stack of tubules or microvilli about $0.03 \mu\text{m}$ in diameter and $0.5\text{--}2.0 \mu\text{m}$ long. This organelle is called the *rhabdomere*, and its microvilli contain the visual pigments, related to rhodopsin. Activation of the rhodopsin by light indirectly causes an increase in permeability of the retinula cell, which responds by depolarization of its membrane but does not generate nerve impulses. Instead, insect photoreceptors are unusual in that they transmit a signal related to the intensity of the light by means of the graded potential that spreads independently along the axon of each retinula cell to the optic lobe.

Insects active by day, such as bees, dragonflies, butterflies, grasshoppers and mantids, as well as some others such as cockroaches, have long rhabdomeres which are fused to form a central *rhabdom* that reaches to the cone tip (Fig. 2). The rhabdom is an absorbing light guide, and pigment granules in the retinula cell cytoplasm around it act as an attenuator of the light when, in the light-adapted state, the pigment moves closely around the rhabdom. In the dark the pigment moves radially away from the rhabdom,

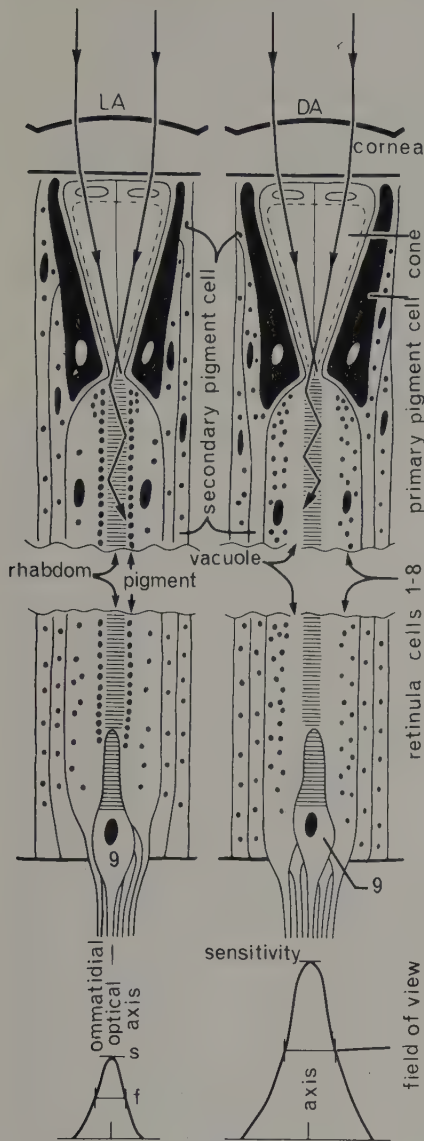


Fig. 2. Ommatidium characteristic of most diurnal insects. The difference between dark adapted (DA) and light adapted (LA) states lies in the distribution of pigment and refractive index around the fused central rhabdom rod. This, by changing its optical properties as a light guide through a critical range, can control its sensitivity (s) and to some extent the size of the field of view (f) as shown at foot of diagram. The 9th retinula cell, lying behind the filter formed by the other 8, can show enhanced detection of the plane of polarization of light, and is the receptor for navigation by this means in the honey bee.

leaving a clear zone of endoplasmic vacuoles around it (compare LA and DA, Fig. 2). Because it has a lower refractive index this zone keeps more light within the rhabdom, so increasing the sensitivity and widening the field of view of each ommatidium in dim light. Each facet looks in a different direction, and the outside world is projected directly upon the optic lobe below.

Muscid flies have quite a different type of eye. Here the rhabdomeres are separate, not fused, and seven different rhabdomeres receive light from seven different directions through each facet. By a marvellous pattern of axon connections, in which each retinula cell terminal makes its own separate contact with the second-order neurons of the most superficial optic neuropile layer (the lamina), the angular co-ordinates of the outside world are reconstructed by summation of graded

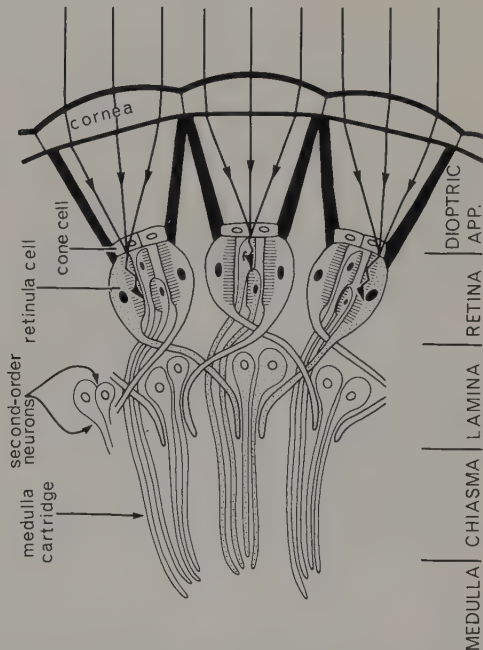


Fig. 3. Eye type of muscid flies. Parallel rays falling on the eye are focused on the distal ends of the separated rhabdomere rods, which are the receptors. Axons of these receptor cells converge, so that excitation from one point in the surrounding world is brought to one place in the optic lobe, as shown by the dotted axons.

potentials at terminals in the first synaptic layer and then again in the second synaptic layer (Fig. 3).

Hemiptera, and a few other groups such as Diptera-Nematocera, Dermaptera and Coleoptera-Staphylinidae, Cerambycidae and Tenebrionidae, have mobile cone cells (*acone eyes*). In the dark-adapted eye the separate rhabdomeres are pressed close to the cornea and the aperture is wide, whereas in the light the rhabdomeres move away from the cornea and pull into a long transparent thread that is surrounded by pigment (Fig. 4). The effect of this extensive movement is to narrow the field of view at the expense of the aperture and sensitivity, but to an extent exactly matched to the ambient light intensity.

The most remarkable range of eyes are those which, despite their small aperture, meet the problem of seeing in dim light as well as daylight. They attempt to compensate for the intensity ratio of about 10^7 between the brightness of sunlight and moonlight. All of these nocturnal eyes have a wide clear

zone between the cones and the rhabdom (receptor) layer, and in almost all of them (except skipper butterflies) this clear zone is crossed in each ommatidium by a light guide which is surrounded by isolating and attenuating pigment during the day. In dim light the pigment moves distally from around this light guide to a space between the cones and, most significantly, leaves the tips of the cones exposed. A wider beam of light can now pass into the clear zone through each cone. Rays entering by many facets now sum upon a single receptor and the aperture becomes 20 to 50 facets wide. The effect is to increase the aperture of the eye and increase sensitivity, usually at the expense of acuity. There is a great diversity in the movement of pigment and of cell bodies in different orders of insects (Fig. 5). In many of these clear-zone eyes the ommatidium has a first converging lens formed by the convexity of the facet and a second converging lens formed by an inhomogeneous refractive index of the cone plus the curvature of the cone tip. This second lens has the effect that a parallel beam of light falling on the eye is partially focused on the receptor layer. The better the focusing, the less the eye has to trade acuity for sensitivity as the aperture of the whole eye opens. Elateridae, Lycidae and Lampyridae, with corneal cones, Hesperioidea and some nocturnal moths with inhomogeneous crystalline cones, have eyes that are excellently focused by the second lens in each ommatidium, as observed by Exner in the firefly *Lampyris* in 1891. Some clear-zone eyes have a reflecting layer below the receptors (*tapetum*), which sends the light a second time through the visual pigment. This causes eyeshine, and when the eyeshine is seen only in line with the source of light the eye must be well focused. For further information on eye structure and physiology see Horridge (1974).

Discussion about what insects see is dependent entirely on the nature of the tests that can be made. *Discriminations* are behavioural tests which show that the animal actually sees differences between relevant stimuli. This applies very well to colours,

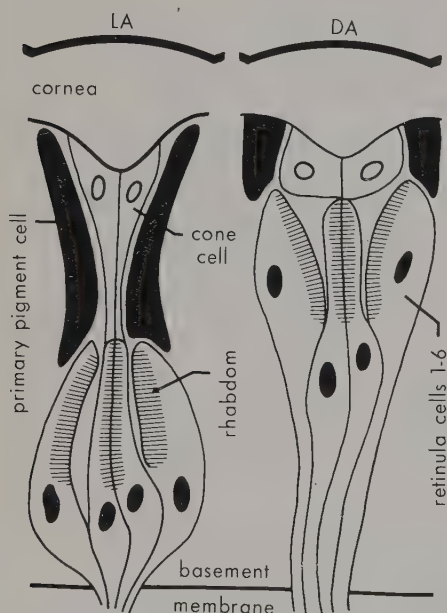


Fig. 4. Ommatidia of hemipteran type of compound eye (*acone eye*) in LA and DA state. Note the control of aperture by extensive cell movement.

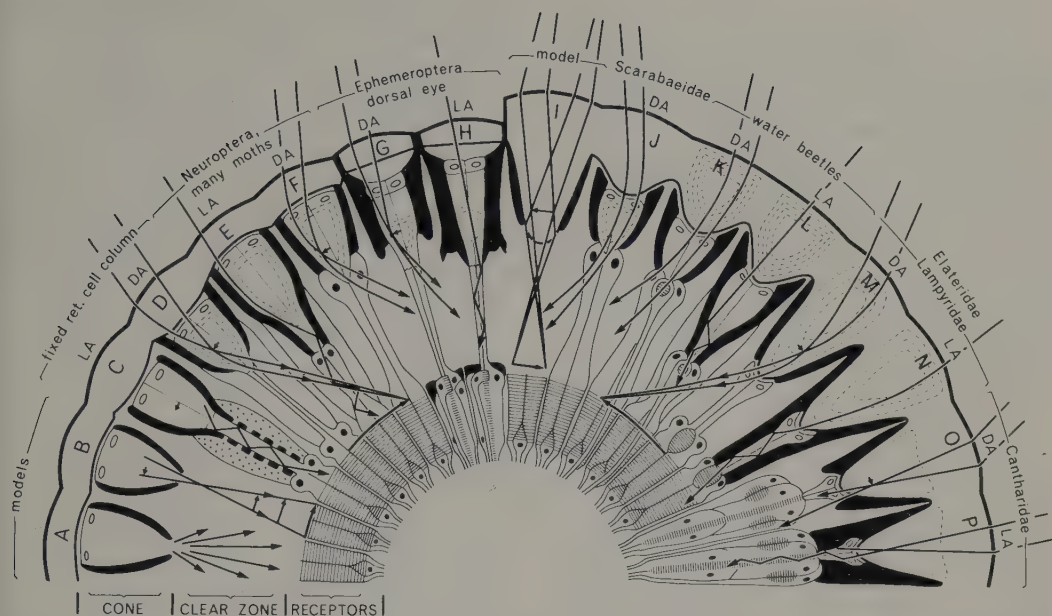


Fig. 5. Ommatidia of eyes adapted for dim light vision by having a clear zone between cornea and receptor layer. The diversity lies in the presence and position of a second lens, and especially in the mechanisms of adaptation to a range of intensity. Retinula cell nuclei are solid black, cone cell nuclei are open circles, significant pigment is solid black, inhomogeneous refractive index is shown by dashed zones, rhabdoms are cross-hatched, and light rays bear arrows. A. Even if light is scattered from the cone tip across the clear zone, there is an increased sensitivity by summation on the receptors. B. The cone tip can act as a pinhole so that a poor image forms on the receptors. This is not known to be functional, but can form artefacts in eye slices examined for images. C, D. Crystalline cone and fixed (retinula cell) light guide, found in some Lepidoptera. Adaptation is by pigment migration around the light guide. Hesperioidea are of this type but permanently DA, and with an excellent focusing of off-axis rays by a second lens within the cone. E, F. Typical neuropteroid type with a column of retinula cells that acts as a light guide and is surrounded by pigment in LA state. Neuroptera, some lower Coleoptera, many moths. Note movement between LA and DA states. G, H. Dorsal eye of Ephemeroptera. Fixed retinula cell column forms a light guide. Focusing is poor and pigment movement small, so the eye is probably suited for a particular ambient intensity. I. When the cornea is very thick, with internally projecting corneal cone, the inner curved surface of the cone acts as a second lens and contributes towards focusing on the receptor layer. J. DA state in many scarabaeoid beetles, with focusing by inhomogeneous crystalline cone, and cell movement as in E, F during adaptation. K, L. In beetles of the families Carabidae, Gyrinidae, Dytiscidae and Hydrophilidae there is, in addition to the other neuropteroid mechanisms, a solitary distal rhabdomere (cross-hatched) which lies directly in the light path of a single facet. In the DA state, light is partially focused across the clear zone upon the receptor layers. M, N. Beetles of the families Elateridae, Lampyridae and Lycidae have inhomogeneous corneal cones, fixed crystalline tracts and extensive pigment migration as shown. The DA eye is well focused, and in the LA eye each ommatidium operates separately by its light guide. O, P. Beetles of the family Cantharidae have a narrow clear zone crossed by a (cone-cell) crystalline tract. In the LA state the eye is apposition only, but in the DA state another set of rhabdomeres catch light that crosses the clear zone obliquely outside the light guide.

including ultraviolet, in some diurnal insects (bees, dragonflies, butterflies), plane of polarization (bees and ants), and intensity. The feature which most limits vision is the size of the field of view of the receptor cells. This ranges from 1–2° in large diurnal insects with apposition eyes, to 5–8° in many light-adapted insects with poor eyes, to 12–40° for

the receptors of dark-adapted eyes with very high sensitivities that operate in dim light. These fields limit the acuity of the eye for regular striped patterns or black objects on a bright background, but much smaller bright objects on a dark background can be picked out.

There is negligible evidence for static form

by Lorenz. The essence of these ideas, which were made available in English by Tinbergen (1951) and Schiller (1957), was that some sort of nervous energy, called *action specific energy*, was released by specific stimuli, acting through an *innate releasing mechanism*, to evoke a characteristic action, the *fixed action pattern*. Apart from the fact that slow-motion photography has shown that the fixity of a particular behaviour may be more apparent than real, the notion of action specific energy has been severely criticized (e.g. by Kennedy, 1972) on the grounds that it is subjective and teleological. The ethologists have also been criticized for failure to take adequate account of the modification of behaviour through experience—that is, to distinguish clearly between the operation of intrinsic and extrinsic factors. Questions as to what components of behaviour may be regarded as innate rather than acquired have been examined more critically since then. Baerends (1959) touched on the genetics of behaviour, especially with regard to the behaviour of hybrid insects, and the behavioural genetics of insects in general has been reviewed by Ewing and Manning (1967) and of *Drosophila* by Parsons (1973).

In the current literature on insect behaviour, teleological concepts such as goals, purpose, drives and motivation are seldom used, probably because insect behaviour is sufficiently amenable to experiment for interpretations to be made in terms of underlying mechanisms.

Work on insects over the last century has shown that some behaviours may be programmed as a strict sequence of elements which appear when appropriate stimuli are provided in a certain order. The traditional example is the provisioning of nests by species of digger wasps (Sphecidae). Such sequences of responses have been described as chains of responses, chains of reflexes, or hierarchies of responses. In some instances the concept of a hierarchy is supported by experimental evidence of a pattern of neural organization, in which the brain has a controlling function by normally exerting inhibition in the absence of stimuli which

release a particular response. A simpler sequence may appear when male Lepidoptera are exposed to progressively increasing concentrations of sex pheromone from females. The successive behaviours may overlap and compound, progressing from movements of the antennae only, to walking with moving antennae, to wing fluttering, to orientated flight, and finally to copulatory movements, some of which are illustrated in Figure 6.

Primers and Releasers

The idea that behaviour is released was put forward by Tinbergen and Lorenz, and is now used widely to discriminate between two different kinds of stimuli: those which *release* behaviour immediately, as opposed to those which *prime* physiological development or some other change of physiological state. Pheromones (p. 35), which are especially important in regulating the behaviour of social insects, may be either primers or releasers (Wilson, 1971). Also the odour of a specific host plant may release oviposition behaviour from an insect, whilst acting separately to prime ovarian development. Riddiford and Truman (in Barton Browne, 1974) have suggested a classification of hormones, too, as either releasers or modifiers according to their mode of influence on behaviour. Releaser hormones were described as those with an immediate effect on behaviour, as when extracts of corpora cardiaca applied to the phallic nerve of *Periplaneta americana* elicit rhythmical bursts of electrical activity which evoke copulatory movements. By contrast, modifier hormones influence behaviour indirectly. For instance, the hormonal influence of the corpora allata is necessary for the development and maintenance of sexual receptivity in females of the grasshopper *Gomphocerus rufus*.

Orientations

An important part of Lorenzian ethology was the separation of fixed action patterns from orientations. The latter were described as the varied *appetitive* behaviours which provided links between fixed, instinctive acts.

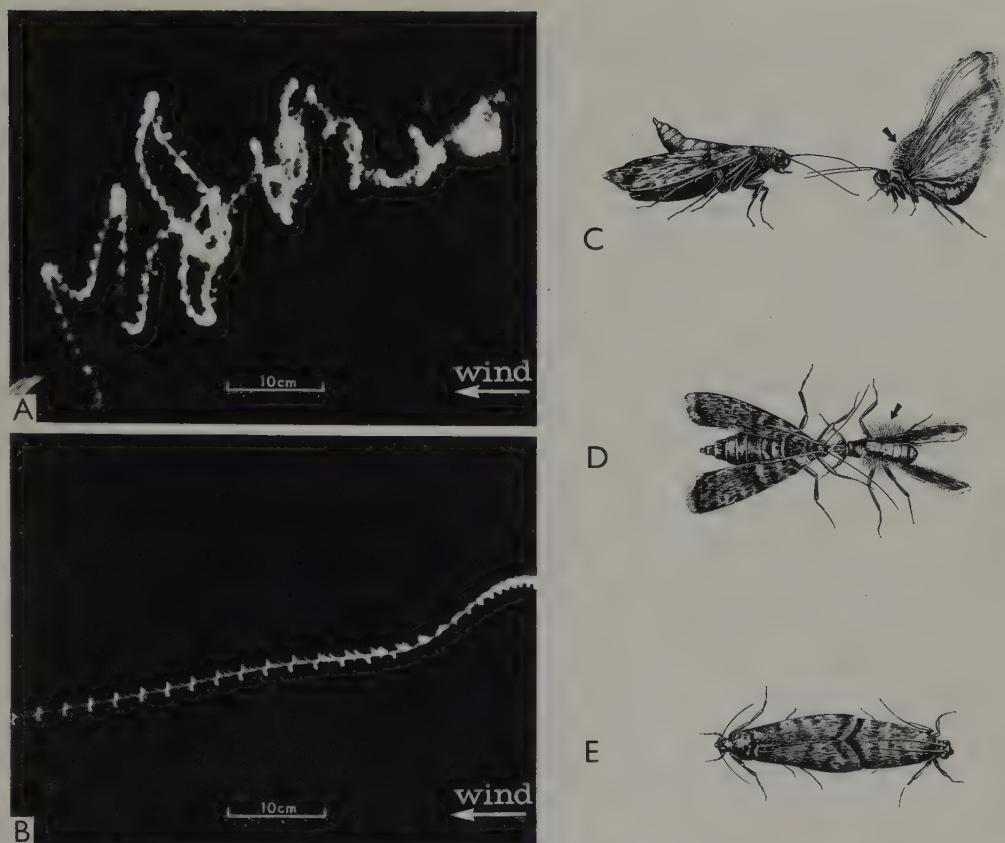


Fig. 6. Orientations in the sexual behaviour of male *Ephestia* spp. (Pyralidae). A, B, photographs of tracks of single male *E. kuehniella* flying in a wind tunnel in response to female sex pheromone. A, plan view showing approach to a 'calling' female held in the centre of tunnel; exposure, 18 sec. B, side view showing more direct upwind flight in air uniformly permeated with pheromone; exposure <1 sec. C–E, a sequence of sexual behaviours in *E. cautella*, ♀ left, ♂ right. C, female in 'calling' position with pheromone gland exposed at the tip of abdomen; a tuft of scent scales (arrowed) stands erect on each fore wing of the male. D, head-to-head with interlocking antennae. E, in copula.

[C–E by G. C. Palmer]

A phase in the experimental study of orientations was rounded off by the classical text of Fraenkel and Gunn (1961), which classified orientations into categories of kinesis, taxes and transverse orientations. In *kinesis*, locomotion is random with respect to the directional properties of the stimulus, but nevertheless results in orientation, for example by a change in velocity in the presence of the stimulus. *Taxes* are directed movements in which the long axis of the body is orientated in line with a source of stimulus. *Transverse orientations* are those made at a temporarily fixed angle to the direction of stimulus, as in

the sun-compass orientations of ants and bees. One type of orientation, *klinokinesis*, has since been rejected by Gunn (in Haskell, 1966, pp. 109–10) on the grounds that it had not been rigorously demonstrated. It had been defined as an orientation achieved by changes in the rate of turning without regard to direction, as determined by changes in the intensity of stimulation and by adaptation, but has since been used in a different sense by Hinde (1970).

Although experiments are a prerequisite for allotting a particular orientation to one or other of the categories, the classification is

not primarily concerned with the physiological mechanisms that effect the orientation; it is sufficient merely to show that they exist.

Fraenkel and Gunn had warned that some orientations did not fall naturally into any of their categories, and confusion has resulted from some attempts to apply the system. The responses of insects to trails of odour in air are an example. These movements have been described in terms of various types of orientation, but most frequently as *anemotaxis* (Haskell, 1966; Kennedy and Moorhouse, 1969; Shorey, 1973). Unfortunately, anemotaxis has been applied to several different patterns of orientation, so at present it seems to be more of a hindrance than an aid to understanding the behavioural processes involved. The responses of an insect to airborne odour may vary according to its mode of presentation (Fig. 6A, B), and it may be that some of them do not fit into any of the categories.

As new techniques have become available, the physiological mechanisms that mediate orientations are being increasingly investigated. For example, Belton (in Barton Browne, 1974) recorded the flight path of male *Aedes aegypti* to sources of sound imitating that produced by the female. He obtained simultaneous electrical records from the Johnston's organ of each antenna (Fig. 2.15B) in relation to sound from different directions, and concluded that the phase relationships and amplitudes of the electrical output of the two Johnston's organs provided sufficient information to account for the observed flight behaviour.

Another approach to orientations is to describe their mechanism in terms of systems dynamics, as used by control engineers (Mittelstaedt, 1962). This approach has been followed in studies of the *optomotor response*, which is movement of the head or body to follow movements in the environment. This behaviour has been interpreted in terms of a continuously running feed-back loop which minimizes the velocity of shift of the visual field relative to the eye. The accuracy of this response to the environment

depends upon the gain within the loop. In active locomotion, the reference point of the loop changes so that movements of the insect relative to those of the environment do not invoke the optomotor response.

The chemicals that affect the behaviour of insects were divided into categories by Dethier and his associates and the scheme extended by Beck (1965) to include other kinds of stimuli. The three terms that follow are those most often used. An *attractant* is a substance to which the insect responds by orientating movements towards the apparent source; a *repellent* elicits an orientated response away from the apparent source; an *arrestant* causes the insect to cease locomotion when in close contact with the apparent source. This classification has proved useful in encouraging a uniform terminology.

Influence of Previous Experience

A given insect kept in a controlled environment may respond differently to the same stimulus when starved or fed, when mated or unmated, or when presented with the stimulus for a second time. The tendency to respond may be modified by external changes such as photoperiod, or by an internal behavioural change such as learning, and these different influences may interact with one another. The ability of an experimenter to predict the responses of the insect is limited, therefore, by his knowledge of the ways in which previous experience influences current behaviour. In general, the experience and its consequences are confined to a single stage in the life history, although some induced behaviours can persist through metamorphosis.

Influence of previous stimulation. The continued presence of a stimulus is usually accompanied by a decline in responsiveness. This effect is seen both in the intact animal and at the level of a single neuron. Hinde (1970) has proposed that a longer-term waning of responsiveness may be considered as *habituation*, as opposed to a shorter-term waning to be called *adaptation*. In neurobiology, and often in behavioural studies,

these terms have been used more strictly: adaptation to describe the waning of responsiveness that follows a single continuous stimulus, as opposed to habituation as the (longer-term) waning that follows the repeated presentation of a stimulus. These concepts are not wholly unambiguous, and the following example seems to fall between the two. Sex pheromones of female *Lepidoptera* elicit spectacular responses from males (p. 8), but exposure of males to sex pheromone tends to reduce their responsiveness to a second exposure several hours later. It has been suggested that this effect is mediated by changes in the central nervous system (CNS) induced by the reception of the stimulus, rather than by sensory adaptation or by the previous performance of a motor act (Bartell and Lawrence, 1973).

There is so much evidence for the influence of the CNS as a mediator of behavioural changes, even in the absence of gross physiological changes, that it is clearly unwise to suppose that conclusions about behaviour can be drawn only from a study of the effects of stimuli on sense organs. For example, a blowfly satiated with water does not extend its proboscis when water touches a labellar hair, but if another labellar hair is touched by a dilute solution of sucrose before stimulation by water, the contact with water elicits proboscis extension. This change in responsiveness to water is interpreted as evidence that a *central excitatory state* is temporarily induced in the CNS. Further, there is evidence that a *central inhibitory state* is induced when a single labellar hair is touched by a salt solution.

The concepts of central excitatory and inhibitory states have been applied to the behaviour of the Colorado beetle, *Leptinotarsa decemlineata*, in more natural feeding situations (Jermy, 1971). When an adult *L. decemlineata* has been deprived of food, it makes excited circling movements following a momentary exposure to the sight and odour of a potato leaf. Further, a larva will normally remain feeding on a potato leaf, but if it ingests a droplet of fluid containing a feeding deterrent which has been placed on the leaf

by the experimenter, it not only stops feeding, but usually moves away and feeding is inhibited for a relatively long time.

Influence of previous behaviour. Up to this point, emphasis has been placed upon the role of external stimuli in releasing behaviour or modifying subsequent behaviour. For a complete understanding of behaviour, however, attention must be paid also to the ways in which different behaviours exert excitatory and inhibitory influences upon one another without the intervention of external stimuli.

The interactions of behaviours in an integrated sequence were discussed by Blest (1960), who showed that the number of rocking movements made by moths (*Automeris aurantiaca*) of a given age on landing after tethered flight was directly proportional to the duration of the flight. On the basis of these and other experiments, he concluded that a reciprocal inhibitory relationship between the systems regulating flight and settling existed within the CNS of *Automeris*, and suggested that similar behaviour might have served as the basis for the 'dances' by which honey bees transmit quantitative information about distant food sources.

Some of the sequences of behaviour shown by alate *Aphis fabae* have been studied extensively (Kennedy and Fosbrooke, in van Emden, 1973, pp. 125-40; Kennedy, in Barton Browne, 1974). In the course of migration, *A. fabae* fly from the host plant, gain altitude, and are carried by air currents. At this stage they show an increasing tendency to orientate more to blue light (sky) than to yellow light (vegetation). As their period of flight increases, their relative preference for light of these different wavelengths gradually reverses and they show an increasing tendency to descend and alight on objects reflecting yellow light. With further increase in duration of flight, they show also an increasing tendency to remain grounded on objects reflecting yellow light placed in their flight path. Landing tendencies appear long before the reserves of energy for flight are exhausted, so are presumably mediated by the CNS. Moreover, flights that follow an initial landing on the leaf of a host plant tend

not primarily concerned with the physiological mechanisms that effect the orientation; it is sufficient merely to show that they exist.

Fraenkel and Gunn had warned that some orientations did not fall naturally into any of their categories, and confusion has resulted from some attempts to apply the system. The responses of insects to trails of odour in air are an example. These movements have been described in terms of various types of orientation, but most frequently as *anemotaxis* (Haskell, 1966; Kennedy and Moorhouse, 1969; Shorey, 1973). Unfortunately, *anemotaxis* has been applied to several different patterns of orientation, so at present it seems to be more of a hindrance than an aid to understanding the behavioural processes involved. The responses of an insect to airborne odour may vary according to its mode of presentation (Fig. 6A, B), and it may be that some of them do not fit into any of the categories.

As new techniques have become available, the physiological mechanisms that mediate orientations are being increasingly investigated. For example, Belton (in Barton Browne, 1974) recorded the flight path of male *Aedes aegypti* to sources of sound imitating that produced by the female. He obtained simultaneous electrical records from the Johnston's organ of each antenna (Fig. 2.15B) in relation to sound from different directions, and concluded that the phase relationships and amplitudes of the electrical output of the two Johnston's organs provided sufficient information to account for the observed flight behaviour.

Another approach to orientations is to describe their mechanism in terms of systems dynamics, as used by control engineers (Mittelstaedt, 1962). This approach has been followed in studies of the *optomotor response*, which is movement of the head or body to follow movements in the environment. This behaviour has been interpreted in terms of a continuously running feed-back loop which minimizes the velocity of shift of the visual field relative to the eye. The accuracy of this response to the environment

depends upon the gain within the loop. In active locomotion, the reference point of the loop changes so that movements of the insect relative to those of the environment do not invoke the optomotor response.

The chemicals that affect the behaviour of insects were divided into categories by Dethier and his associates and the scheme extended by Beck (1965) to include other kinds of stimuli. The three terms that follow are those most often used. An *attractant* is a substance to which the insect responds by orientating movements towards the apparent source; a *repellent* elicits an orientated response away from the apparent source; an *arrestant* causes the insect to cease locomotion when in close contact with the apparent source. This classification has proved useful in encouraging a uniform terminology.

Influence of Previous Experience

A given insect kept in a controlled environment may respond differently to the same stimulus when starved or fed, when mated or unmated, or when presented with the stimulus for a second time. The tendency to respond may be modified by external changes such as photoperiod, or by an internal behavioural change such as learning, and these different influences may interact with one another. The ability of an experimenter to predict the responses of the insect is limited, therefore, by his knowledge of the ways in which previous experience influences current behaviour. In general, the experience and its consequences are confined to a single stage in the life history, although some induced behaviours can persist through metamorphosis.

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to be of shorter duration than those that follow landing on a green card or the leaf of a non-host plant. In discussing his results, Kennedy uses a terminology taken by analogy from Sherrington's work on the successive induction of antagonistic reflexes in mammals.

Gross physiological changes. Many physiological changes, such as those that follow feeding and mating, are known to be mediated by hormones and, as the changes occur, hormones may also act on the nervous system to influence behaviour, including the evocation of eclosion, migratory, sexual and parental behaviours. While many hormonal influences on behaviour have been demonstrated (reviews in Barton Browne, 1974), the mechanisms underlying the resulting changes are only partially understood. For example, two antagonistic hormonal systems have been implicated in the control of marching behaviour of fed *Locusta migratoria* hoppers in the *gregaria* phase: a factor from the corpora cardiaca which generally stimulates marching, and one from the prothoracic glands that is generally inhibitory. This knowledge cannot, however, explain the full complement of variations of behaviour associated with phase changes in *L. migratoria* (Haskell *et al.*, 1965). Also, when *L. migratoria* has fed, a hormonal factor from the corpora cardiaca mediates the closure of pores on the terminal sensilla of the maxillary palps, which consequently have reduced sensitivity as chemoreceptors for an hour or so after a complete meal. This is one of the many mechanisms that control feeding.

On the other hand, studies of regulation of feeding in blowflies have not provided satisfactory evidence of hormonal control. When *Phormia regina* is deprived of food, its behaviour changes so as to increase the probability of an encounter with food (Gelperin, 1971); locomotor activity increases, and 'searching' movements follow the consumption of a droplet of sugar solution too small to satiate the fly. In addition, with increasing food deprivation, there is a decrease in the threshold concentration of sugar solution that

elicits proboscis extension when applied to the tarsi of the fly. This effect cannot be explained in terms of changes in sensitivity of sense organs on the tarsi; it probably results from the integration within the CNS of inputs from distension of the fore gut and abdomen.

In most strains of *Lucilia cuprina*, females will not accept a male before they have had a protein meal or after they have mated, whereas sexual activity of males does not depend upon a protein meal (Bartell *et al.*, 1969). In insects in general, an inhibitory effect of mating upon subsequent mating by females may be mediated by mechanical stimuli provided by a spermatophore in the bursa copulatrix, by the presence of sperm, or by substances from the male accessory glands which pass through the bursa into the blood of the female and act upon the nervous system.

Induced host acceptance. It has been demonstrated convincingly that the larval experience of a hymenopteran parasitoid in a particular species of host may modify its responses as an adult to favour infestation of the host species on which it was reared. It appears, however, that not all species of parasitoids may be so conditioned. Induction of specific feeding habits has also been shown in phytophagous insects. David and Gardiner (1966), working with larvae of the cabbage butterfly, *Pieris brassicae*, which feeds in the natural state upon plants containing thioglucosides, found that many larvae would feed and grow to maturity on an artificial diet which lacked thioglucosides, provided they were placed upon it from the time of hatching. Larvae reared to the fifth instar on fresh cabbage would not accept an artificial diet even if it contained a thioglucoside, although larvae reared on any diet accepted cabbage leaves. This work shows that seemingly specific food preferences may be modifiable, and that the acceptability of food may be determined by more than the presence or absence of a single 'token' stimulus.

Schoonhoven (in van Emden, 1973) showed, by electrical recordings from chemoreceptors on the maxillae of larval *Manduca*

sexta (tobacco hornworm), that they had different levels of responses to various plant substances after feeding upon different diets. These results permitted an explanation of induced host preference in these larvae in terms of changes in the sensitivity of their sense organs. An electrophysiological study of sense organs on the mouth-parts of *Pieris brassicae* larvae, however, showed no significant differences between insects fed on different diets. There is also some evidence for the induction of specific oviposition preferences in *Manduca sexta* following larval feeding on either potato or tomato plants (Yamamoto and Fraenkel, 1960).

It must be stressed that these conditioning effects are reversible and do not demonstrate the inheritance of acquired behaviour. It is conceivable, nevertheless, that induced host preference might play a part in the spatial isolation of different populations of the same species, in which genetic differences might then become fixed by natural selection.

Learning and memory. There is no unambiguous or generally accepted definition of learning. Alloway (1972) began a review on learning and memory in insects with the idea of learning as a relatively permanent change in behaviour which occurs as a result of practice, and of memory as the retention of learning. Many species of insects have been shown to learn (Thorpe, 1963). Some workers have considered the induction of specific host preference as learning, others not. It has been shown that learning may persist through metamorphosis.

Most studies of learning in insects have been made with honey bees which are trained to associate a visual or olfactory stimulus with the presence of food (reviews in Barton Browne, 1974). The association occurs as the bee finds the food source, and curiously, they associate non-floral odours more rapidly with food than floral odours. Memories with three different retention times are known in the process of olfactory learning in the honey bee. The site of the shortest olfactory memory (the sensory memory) is in the two antennal lobes of the brain, and the other

two, the short-term and the long-term, are properties of the mushroom bodies which receive information from the antennal lobes. Memory in honey bees may be time-linked, manifesting itself only at intervals of 24 hours.

A phenomenon that fits the strictest definition of learning has been demonstrated in headless *Periplaneta americana* and *Schistocerca gregaria* (Hoyle, 1970). The headless insects learnt to adjust their leg posture so as to avoid electric shocks. In *Schistocerca* this learning was associated with an increased rate of discharge in nerves that excited the coxal adductor muscle. Horridge (1968) considered that the capacity to evolve learning may exist in all interneurons, especially those involved in feed-back loops.

Neural Basis of Behaviour

An introduction to the physiology of insect behaviour was provided by Bursell (1970). The structure of the nervous system in relation to function has been considered by Bullock and Horridge (1965), Roeder (1967) and Howse (in Barton Browne, 1974). It is generally accepted that even the most complex behaviours shown by insects are controlled and integrated by localized groups of neurons, although many questions about the degree of localization of specific functions remain unanswered. There is a positive correlation between the volume and neuronal complexity of the corpora pedunculata (mushroom bodies) and increasing behavioural complexity, especially in the capacity to learn. Progress in this area is closely linked to the development of new techniques. For example, a cobalt filling method which shows the branching complexity of any chosen neuron in its entirety (Fig. 7) has been used by Altman and Tyrer (in Barton Browne, 1974) to correlate the ontogeny of parts of the nervous system with the ontogeny of simple behaviours.

At present, neurobiologists tend to study the structure and function of sense organs and the physiological basis of the simplest actions known. Such movements are some-

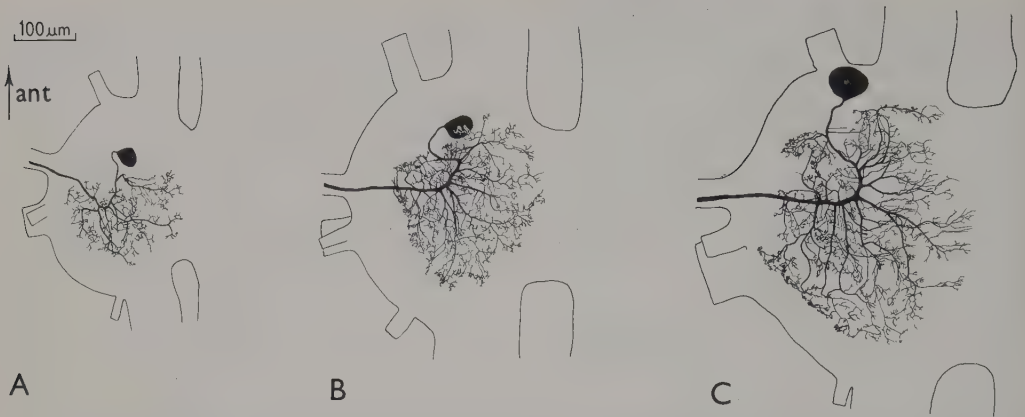


Fig. 7. The development of a motor neuron in the mesothoracic ganglion of the Australian plague locust, *Chortoicetes terminifera*, through larval instars (A, B) to the adult (C); this neuron provides rhythmical bursts of impulses to tergosternal flight muscles (after Altman and Tyrer, in Barton Browne, 1974).

times called *fixed motor patterns*, a concept which appears to overlap with the fixed action patterns of ethology but derives from developmental studies on vertebrates (Tinbergen, 1951). Fixed motor patterns are thought to be elicited by a central programme of nerve impulses, and there is speculation that central programmes are evoked through the agency of command pathways and perhaps even single command neurons.

Central programming has been demonstrated in locusts in extensive studies on the neural control of flight, which is maintained by rhythmical bursts of spike impulses with a minimum of proprioceptive feed-back. These impulses originate from oscillatory systems within the thoracic ganglia. Oscillatory systems have been implicated, also, in the neural control of walking, breathing and stridulation (Miller, in Barton Browne,

1974). Neurons that originate rhythmical activity have been identified in Crustacea but not yet in Insecta. The control centres of circadian rhythms, however, appear to be endocrine and quite distinct from neural oscillators. Writing on cellular mechanisms underlying behaviour, Hoyle (1970) noted that more studies have been made on sensory input than motor output, and presented the view that a science of neuroethology existed, although still in its infancy. Less optimistic reviewers have pointed out that the mechanisms whereby different patterns of behaviour are co-ordinated are not understood at all at the cellular level.

ACKNOWLEDGMENTS. This section was written with guidance from Drs L. B. Barton Browne, I. M. Mackerras, R. J. Bartell, and P. M. Barrer, who also provided Figure 6C-E.

CYTOGENETICS

by M. J. D. WHITE

Since the main volume was written there have been numerous advances in cytogenetics, many of them based on insect material. In the present summary, work on Australian species or by Australian authors will be emphasized. The general field of animal cytogenetics has been recently reviewed by White (1973), while Peacock (1973) has discussed fundamental aspects of chromosome structure and units of function.

Chromosomal Mechanisms in Race and Species Formation

The role of chromosomal reorganization in evolution and, more specifically, of chromosomal rearrangements in riation and speciation, has been much discussed in recent years. Work on the Hawaiian *Drosophilidae* (Carson *et al.*, 1970) has demonstrated that over 700 species have evolved in an 'explosive' manner in less than five million years. There are a number of so-called homosequential complexes of species, the members of which exhibit no visible differences of karyotype, down to the finest details of the banding pattern in the polytene chromosomes of the salivary-gland nuclei. This is proof that major structural rearrangements of the karyotype such as inversions and translocations are not a *sine qua non* for speciation (although even in these instances one is forced to wonder whether there may not have been some structural changes in the heterochromatic sections which, because of under-replication, cannot be analysed in the polytene chromosomes).

Even in *Drosophila*, however, the most closely related species usually differ in respect of structural rearrangements (mainly paracentric inversions); and this is also true of other genera of Diptera, such as *Chironomus* and *Anopheles* (Davidson *et al.*, 1967), in which the existence of polytene

chromosomes permits a much more detailed type of cytogenetic investigation than is possible in other orders. Likewise, in these other orders, such as Orthoptera (John and Hewitt, 1968; White, 1974a), Phasmatodea (Craddock, 1972), Lepidoptera, Coleoptera, Hymenoptera (Crozier, 1970) and others, visible karyotypic differences between closely related species are the rule, and instances of related species with karyotypes that could be homosequential are rare. This situation raises the question whether speciation is not, in general, accompanied by the establishment of chromosomal rearrangements, even though this may not be true of the homosequential species complexes. However, even if this question can be answered in the affirmative, it would not necessarily follow that chromosomal rearrangements frequently play a direct causative role in speciation by furnishing the basis for genetic isolating mechanisms. The relationship could, in fact, be the other way about: incipient species populations, which must frequently consist of a relatively small number of individuals, might provide exceptionally favourable circumstances for the establishment of certain types of chromosomal rearrangements.

It is not only distinct biological species that differ in karyotype; many species consist of several chromosomal races that exhibit differences in chromosome number or form. Deciding where to draw the line between races and species may be extremely difficult, but we prefer to recognize races rather than species where there is a considerable degree of interfertility and where it appears that hybridization occurs on a considerable scale in nature (and is effective in leading to introgression of genetic material because of fertility of the F_1 hybrids).

Because of the extent of variation in population structure, life cycles, vagility, and

importance and type of ethological isolating mechanisms and other factors, we should not expect any single model of the speciation process to be universally applicable. Two classical models of speciation have been designated *sympatric* and *allopatric*. The sympatric model envisages sub-populations of a species within a geographic area becoming adapted to different habitats or ecological niches within the environment of the area as a whole, and ultimately diverging genetically to become distinct species. The allopatric model involves geographical separation of sub-populations, peripherally or otherwise, which can then evolve independently in isolation from one another. The critical aspect is, of course, the amount of gene-flow between the diverging populations. If, in a case of sympatric speciation, the separation of the habitats were complete enough and the vagility of the individual organisms low enough, then we might speak of 'microallopatry'.

Arguments against sympatric speciation have been marshalled by Mayr (1970). After a mathematical consideration of the evidence, Maynard Smith (1966) concluded that 'the crucial step in sympatric speciation is the establishment of a stable polymorphism in a heterogeneous environment. Whether this paper is regarded as an argument for or against sympatric speciation will depend on how likely such a polymorphism is thought to be, and this in turn depends on whether a single gene difference can produce selective coefficients large enough to satisfy the necessary conditions.'

A third model of speciation, based on the role of certain types of chromosomal rearrangements as genetic isolating mechanisms, was put forward by White *et al.* (1967) and White (1968b). This *stasipatric* model was developed initially on evidence from the *viatica* group of morabine grasshoppers in South Australia, but is now supported by a number of other examples, not only in insects but also in some Crustacea, lizards and small mammals. The ten chromosomal races of the Australian phasmatid *Didymuria violescens* (Craddock, in White, 1974a, pp. 24-42)

seem to provide especially strong evidence for it.

The concept of stasipatric speciation is that of chromosomal rearrangements which are adaptive in the homozygous condition but lower the fecundity of heterozygotes establishing themselves in small local populations within the general area occupied by the species. If they then extend their range, we will have a new cytological race which has taken over part of the total range of the species. Where it makes contact with the original form there will be a narrow zone of overlap within which adaptively inferior hybrids will occur. Distribution patterns of this type, where two taxa overlap and hybridize in a zone which may be only a few hundred metres in width, have now been described in many groups of organisms and have been called *parapatric* by some authors. Key (1968, and in White, 1974a, pp. 43-56) has referred to the zones of overlap in such cases as *tension zones*.

It has not been suggested that the stasipatric mode of speciation is a universal one. In all probability it can occur only in organisms of extremely low vagility. Flying insects such as *Drosophila* are far more likely to show classical allopatric speciation, and some phytophagous insects with extreme host specificity (e.g. Tephritidae) may exhibit sympatric speciation. The main indications that stasipatric speciation is occurring, or has occurred, are the parapatric type of distribution, the existence of cytotaxonomic differences between the taxa which lead to abnormalities of meiotic segregation in the heterozygote, and an overall pattern of distribution in which the more recently derived taxa (races or species) occupy a central position, with the ancestral taxon or taxa peripheral to them. This central-peripheral type of distribution is relatively clear in both the *viatica* group of morabine grasshoppers and the *Didymuria* stick-insects.

Key, in the papers cited above and on p. 25, while accepting the general hypothesis of a chromosomal rearrangement basis for speciation in cases like the *viatica* group, has argued that the establishment of a rearrange-

ment that provides the basis for a genetic isolating mechanism is more likely to occur in a peripheral colony of a species than in one more centrally located. Thus he views the origin of a new chromosomally distinct taxon as more likely to take place allopatrically, by invasion of unoccupied territory by a new chromosome race. White (1974a, pp. 57-68) has given some reasons why this process, if it occurs, is likely to be rare by comparison with the origin of a new taxon by the stasipatric process within the original range of the species.

The particular types of chromosomal rearrangements that have been successful in evolution, whether at the level of chromosomal polymorphism in the population or at that of fixation in phylogeny, vary greatly from group to group. Thus in one genus, family or order we may find that numerous paracentric inversions have succeeded in establishing themselves, whereas in another it is duplications of heterochromatin that have been successful, and in yet another fusions of acrocentric chromosomes to form metacentrics (p. 75). These regularities, which sometimes extend over major taxonomic groups, have been ascribed to a principle of *karyotypic orthoselection*. Possible causes for these broad tendencies of karyotypic evolution have been discussed by White (1974b). They may include factors internal to the karyotype itself (i.e. the DNA architecture of the chromosomes) and others arising at the level of the cell, the individual and the population.

Chromosomal Polymorphism in Natural Populations

The era in which the role of chromosomal polymorphisms in natural populations was ascribed to simple heterosis (p. 77) is gradually being succeeded by one in which it is becoming increasingly evident that naturally occurring inversions and other chromosomal rearrangements have very complex biological properties and, when present in high frequencies in the population, may be adaptive to particular ecological niches. Niche adaptation and frequency-dependent selection are

thus coming to be recognized as major factors in maintaining genetic equilibria in natural populations, as far as cytogenetic polymorphisms are concerned. In mosquitoes, individuals with different karyotypes may be differentially attracted to alternative vertebrate hosts, and in some instances may even emerge from the pupa at different times of the day (Coluzzi, 1972). As copulation takes place very soon after emergence, this may lead to non-random mating.

The situation is probably basically similar with regard to the adaptive role of many polymorphisms involving supernumerary chromosomes (called B-chromosomes by some authors). In this case, however, the mode of inheritance of these extra chromosomes usually deviates statistically from the Mendelian rules (Jackson and Cheung, 1967) and they may have 'accumulation mechanisms' at various stages in the life cycle, which would cause them to increase in frequency in each successive generation if this tendency were not opposed by natural selection. It has been claimed that some supernumerary chromosomes are entirely deleterious and are only maintained in the population by their accumulation mechanisms.

The old dilemma as to how groups like the Chironomidae, Culicidae and certain species of grasshoppers, all of which have chiasmata in the males, avoid paying the penalty for inversion polymorphism (due to the production of inviable chromosome strands by crossing over between mutually inverted segments) has now been disposed of. It is clear, as a result of the work of Martin (1967) and others, that in such insects the mutually inverted segments simply do not synapse homologously at meiosis, or only do so in a small proportion of the cells. Instead they pair non-homologously so that no inversion loops are present at pachytene. Since crossing over is only possible between homologously synapsed strands, this mechanism prevents the formation of gametes carrying inviable or lethal chromosomes.

Anomalous Chromosome Cycles

It is well known that extremely anomalous

chromosome cycles and cytogenetic mechanisms occur in certain families of nematocerosous Diptera (Sciaridae, Cecidomyiidae, Chironomidae-Orthoclaadiinae) and in the scale insects. The chromosome cycles of a number of Australian scale insects belonging to the family Eriococcidae have been described by Brown (1967). In these insects both sexes are diploid, but in the males the paternal chromosomal set is heterochromatic in the somatic nuclei, and must be presumed to be genetically inactivated (there is genetic evidence of inactivation in mealy bugs of the genus *Planococcus*).

Parthenogenesis

The cytogenetic mechanisms of parthenogenesis in insects have been reviewed by White (1973). Porter (1971) has described the situation in the Australian chironomid *Lundstroemia parthenogenetica*, a triploid species ($3n=9$) which is a permanent heterozygote for two inversions and a deletion; maturation in the oocyte is of the apomictic type, with no reduction of chromosome number.

Further work by White and Webb (1968) and White *et al.* (1973) has led to a more complete understanding of the genetic system of the Australian parthenogenetic grasshopper *Moraba virgo*. This species, now

known to inhabit an extensive area in western New South Wales and a smaller area south of Kalgoorlie, Western Australia, is a diploid, with $2n=15$ (the karyotype is illustrated in Fig. 3.6). It is now clear, however, that the chromosomes originally interpreted as the 'CD' pair of autosomes (and so labelled in Fig. 3.6) are in fact sex-chromosomes, and that the chromosomes formerly regarded as X-chromosomes are actually the CD pair. *M. virgo* is descended from a bisexual ancestor which had an X_1X_2Y (σ): $X_1X_1X_2X_2$ (ϕ) sex-chromosome constitution. However, the actual constitution of *virgo* is $X_1X_1X_2O$ (where O represents the absence of a chromosome). The small unpaired chromosome formerly designated 'm₂' is in fact the X_2 of the bisexual ancestor. This reinterpretation of the karyotype became possible when an $X_1X_2Y:X_1X_1X_2Y_2$ species related to *virgo* was discovered in Western Australia (although this is not the actual ancestor of *virgo*, which is probably extinct). The karyotype of *M. virgo* is extensively heterozygous for late-replicating DNA segments, a most peculiar feature made possible by the complete absence of genetic crossing-over at meiosis. *M. virgo* has now been successfully crossed in the laboratory with males of two related bisexual species; the progeny are male and female triploids.

4

REPRODUCTION AND METAMORPHOSIS

by H. E. HINTON

Embryology

Modern reviews of hexapod embryology have been published by Counce and Waddington (1972) and Anderson (1973).

Post-embryonic Growth

The course of events during growth and metamorphosis described on pp. 91-4 has been examined more closely by Hinton

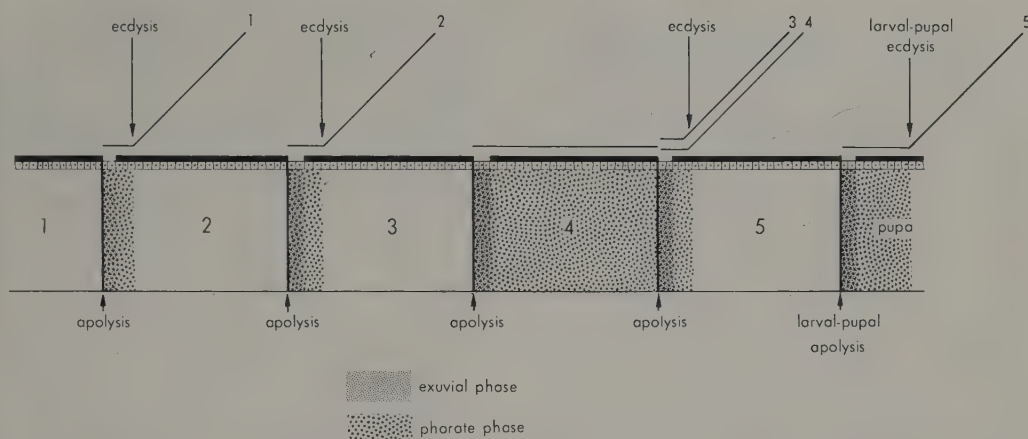


Fig. 8. The exuvial and cuticular phases of a graçillariid moth during the larval and pupal instars (after Hinton, 1971).

(1971), Wigglesworth (1973a) and Hinton (1973), in which other references to recent work may be found.

As there has been confusion, it is necessary to state first what is meant by the terms 'stage' and 'instar'. The *stages* of an insect are the egg, the larva, the pupa (in endopterygotes), and the adult. The *instars* are the subdivisions of the stages: several larval, one pupal, and usually one adult (two in Ephemeroptera, many in Apterygota). Stages and instars begin at apolysis and end at apolysis (p. 93).

Apolysis is initiated by ecdysones, ecdysis by quite different hormones called eclosion or exuviation hormones (Hinton, 1973). Between each apolysis and the succeeding ecdysis the insect is in a pharate phase enveloped by the old cuticle of the previous instar. The pharate phase itself, however, consists of two quite different phases which it is sometimes essential to distinguish. The first is an *exuvial phase*, originally recognized by Janet, when the old cuticle has been detached from the epidermis and the outer surface of the epidermis is naked (Fig. 8). During the exuvial phase the epidermal cells are free to undergo division and rearrangement. The exuvial phase comes to an end and is succeeded by a *cuticular phase* with the secretion of cuticular plaques, mostly at the ends of the epidermal

microvilli, and their fusion into a continuous layer of epicuticle. Although the existence of an exuvial phase has often been denied, careful work with the electron microscope on a variety of insects during the last few years has left no room to doubt its reality. In *Tenebrio molitor* the exuvial phase of the pharate adult lasts about two days (Delachambre, 1970). Its duration in a number of other insects has been given by Hinton (1971), who has suggested that there may be a relation between the duration of the exuvial phase and the extent to which the epidermis is remodelled. At apolysis when the exuvial phase is initiated, the insect may bear little resemblance to its final form after remodelling is completed. For instance, at the beginning of the exuvial phase of the pharate adult stage of, say, a moth, the animal looks like a pupa and is structurally like one. But in order to define the stages and instars clearly, it is necessary to use a discontinuous process, i.e. apolysis or the detachment of the cuticles.

The first indication of apolysis is a separation and decrease in density of the fibrils in the subcuticle between the epidermis and the innermost lamellae of the procuticle. The subcuticle contains microfibrils not organized into lamellae (Delachambre, 1967). In due course the space formerly occupied by the subcuticle becomes the primary exuvial space

that contains a more or less homogeneous moulting fluid. This space is later enlarged as the inner layers of the procuticle are digested and, in some instances perhaps, also enlarged by a retraction of the epidermis. After the destruction of the subcuticle the epidermis is naked. It therefore appears that the plasma membrane of the epidermal cells provides sufficient protection against the enzymes that first digest the subcuticle and later the inner layers of the procuticle. At a later stage the moulting (ecdysial) membrane may protect the epidermis against other proenzymes that are later activated in the moulting fluid, but perhaps its chief function is to provide mechanical protection for the naked epidermis during the exuvial phase.

The secretion of the cuticular plaques at the ends of the epidermal microvilli, which heralds the beginning of the end of the exuvial phase, has now been described in many orders, e.g. Blattodea (Bullière, 1973), Isoptera (Noirot and Noirot-Timotheé, 1971a), Orthoptera (Rinterknecht and Levi, 1966), Hemiptera (Filshie and Waterhouse, 1969), Coleoptera (Delachambre, 1967, 1970; Zacharuk, 1972), Lepidoptera (Locke, 1966; Gemne, 1971), and Diptera (Filshie, 1970). Characteristically the plaques are 10 to 15 nm thick, and they are trilaminar, although in *Locusta* they are said to contain 7 layers at first and later 5 (Delachambre, 1970). Most writers speak of the plaques later fusing to form a continuous trilaminar layer, but it is not evident that fusing is the right word for the deposition or self-assembly of further trilaminar material so as to join the existing plaques into a continuous trilaminar layer. Cell division is very generally confined to the exuvial phase, and it may perhaps occur up to the formation of a continuous trilaminar layer. I have not been able to find mitoses during the late cuticular phases of the pharate stage, but cell division has occasionally been reported when the cuticle is well developed, e.g. in *Calpodes*. This matter clearly requires further investigation.

There is an antero-posterior gradient in the time of apolysis, which generally occurs a

few minutes to an hour or so sooner at the anterior than at the posterior end. In the Diptera-Cyclorrhapha, which are among the most specialized of all insects, the difference in time between the larval-pupal apolysis at the anterior and posterior ends is exceptionally great. In *Musca domestica* bred at 30°C the difference between the completion of the larval-pupal apolysis anteriorly and posteriorly ranges from 2 to 5 hours, and in *Sarcophaga bullata* bred at 24°C it is as much as 8 hours (Fraenkel and Bhaskaran, 1973).

There is some evidence that nervous connections are maintained to the old cuticle during the pharate phases. For instance, the pharate pupa of *Simulium* feeds for some days before it spins its cocoon (p. 94). Blaney *et al.* (1971) have shown that after apolysis in *Locusta migratoria* the scolopales extend across the space between the old and new cuticles and protect the dendrites, which remain in a functional condition until shortly before ecdysis. It now appears that the dendrites of the sense organs are the only exception to the rule that there are no living connections between the old and new cuticles during the pharate phases.

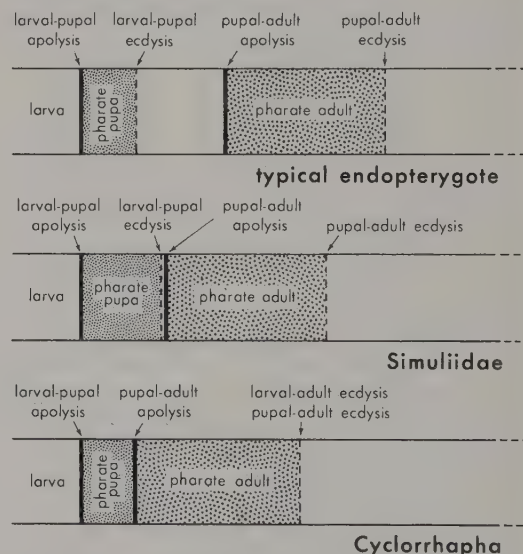


Fig. 9. Variations in the times of apolysis and ecdysis during metamorphosis of endopterygote insects (after Hinton, 1971).

The difficulties inherent in using ecdysis instead of apolysis as the event that marks the beginning of new instars or stages in arthropods have been described by Hinton (1971). Objections to using apolysis in this way have been discussed by Wigglesworth

(1973a), and a detailed reply to the points made by Wigglesworth has been given by Hinton (1973). Some variations in the relationship between apolysis and ecdysis are illustrated in Figure 9.

5

GENERAL BIOLOGY

by K. R. NORRIS

Cave Arthropods

A. M. Richards (1971a) has reported on 95 species of arthropods from 47 caves in the Tertiary limestone of the Nullarbor Plain in southern Australia. Most are troglloxenes or troglrophiles, and only 6 are troglobites (p. 110): a centipede, an isopod, three spiders and a cockroach, *Trogloblattella nullarborensis* (Fig. 5.6). This insect has now been found in nine Nullarbor caves from the 'twilight zone' into total darkness up to 4.8 km from the entrance. There appear to be limited opportunities for it to disperse from cave to cave via subterranean fissures, but it may perhaps be able to travel overland at night, and sinkholes and the burrows of rabbits and wombats could provide temporary refugia during the day-time.

The permanent cave fauna is totally dependent on the fauna and flora of the open plain for its ultimate energy sources. About two-thirds of the Nullarbor cave arthropods are predators, and the most important sources of food for the remaining species, which form their prey, are bird and bat guano, fungi, decaying vegetation washed or blown into the caves, and the carcasses of vertebrates and invertebrates that become trapped or die there naturally.

No troglobitic Coleoptera are known from

the mainland, but some have been found in Tasmania. For many years *Idacarabus troglodytes* (Carabidae-Merizodinae) was the only one known, but a second species, *I. cordicollis*, has recently been discovered in a neighbouring limestone area in southern Tasmania. Troglobitic Carabidae-Trechinae, which are common predators in caves in

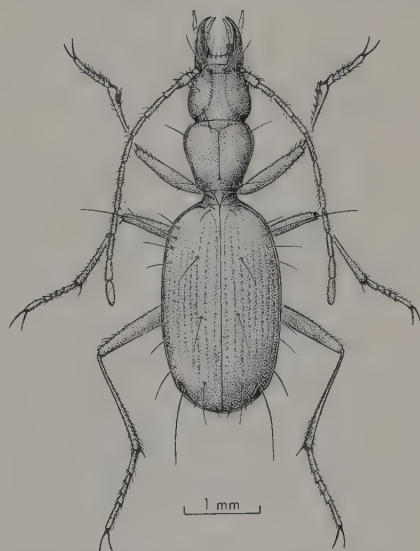


Fig. 10. A troglobitic cave beetle, *Goedetrechus mendumae*, Carabidae-Trechinae.

[S. Monteith]

presence every year. Perhaps most important of all, the recycling of minerals and nutrients is retarded and progressive impoverishment of the soil is consequently accelerated.

G. F. Bornemissza called attention to the magnitude of the problem in 1960 and proposed that remedies should be sought in Africa, where there is a large and varied fauna of more than 2,000 species of scarabaeine dung beetles, many of which are specifically adapted to the large, wet pads of elephants, buffalo and other cattle-sized

herbivores of the continent. This programme is now being vigorously implemented, with the successful establishment of species such as *Onthophagus gazella* in tropical and sub-tropical Australia and of *Euoniticellus intermedius* in more southerly inland regions. In areas that these beetles have fully populated, there has been a marked acceleration in the rate of disappearance of cattle dung at times when soil moisture levels are adequate (Ferrar, 1973).

6

PRINCIPLES OF CLASSIFICATION AND NOMENCLATURE

by K. H. L. KEY

Numerical Taxonomy

Extensive studies on the principles and methodology of numerical taxonomy have been undertaken during the past five or six years (see Sneath and Sokal, 1973). The underlying philosophical principles have emerged largely unscathed, and indeed reinforced, but significant practical limitations have become evident as the techniques have been applied to the classification of different groups of organisms.

The most disconcerting finding has been that widely different classifications may result from the use of different coefficients of resemblance and different sorting strategies that nevertheless appear to have equal, or nearly equal, methodological plausibility. Similar differences may be produced when different, numerically adequate, suites of characters are chosen, e.g. larval v. adult characters, male v. female, or external v. genitalic. Where the taxa to be classified are

numerous and reasonably diversified, as in the species of a medium-sized subfamily, serious difficulties may also arise through the prevalence of characters that are highly diagnostic within one section of the group, but inapplicable in others. These problems arise most often in groups exhibiting poor structure, where extensive evolutionary convergence and parallelism may be suspected. The upshot unfortunately tends to be that numerical taxonomy is of little help when it is most needed.

The claims of 'phylogenetic' taxonomy, as usually understood, have not gained in credibility. However, attempts have been made by phenetic taxonomists to derive phylogenies by the rigorous application of modified numerical techniques; the success of these attempts seems open to question.

The conclusion is now inescapable that there is no 'best' classification (cf. L. Johnson, 1968), much less a 'correct' classification.

We have to be content to achieve a 'good' classification, and this must incorporate criteria of convenience as well as phenetic distance. At the generic level, for example, we should aim at a certain level of discreteness, the presence of one or more necessary and sufficient attributes, a reasonable level of phenetic homogeneity within the genus, avoidance of many monotypic or very large genera, the availability of diagnostic characters in both sexes, and ideally of characters observable without dissection.

Species and Speciation

Controversy has continued on the possibility that speciation may occur without antecedent geographical isolation. In this connection some prominence has been attained by cases of the 'parapatric' distribution of races and species, in which the respective ranges come into contact and overlap to a uniform, but only very restricted, depth. It seems that parapatry may be a not uncommon consequence of secondary contact between a parent population and a divergent allopatric isolate where the resulting hybrids show reduced fitness, and especially where the divergence has involved chromosomal rearrangements in weakly vagile animals. In such cases it has been argued that Dobzhansky's concept of selection for premating isolating mechanisms could not operate, because of the small size of the population in which the hybridization is occurring, relative to the populations as a whole. However, another mechanism, leading to a reinforcement of *postmating* genetic isolation is available, in the form of progressive accretion on the 'tension zone' of additional genetic modifications that may have become fixed on one side or the other (Key, in White, 1974a, pp. 43–56; see also Bazykin, 1969). M. White (1968b, 1973, and see p. 16) interprets this situation as involving origin of the new genotype at a single point *within* the distribution of the parental one rather than allopatrically—a process for

which he uses the term 'stasipatric' speciation. Other models, also not requiring geographic isolation, have been postulated, but it is doubtful whether they can be substantiated (Mayr, 1970).

Study of parapatric distributions and of 'hybrid zones' has revived discussion as to the degree of gene flow that is to be permitted between what we are to regard as species. Short (1969) has examined this question in birds and Key (in White, 1974a) in the context of morabine grasshoppers. The issue is not really a biological one, but rather a question of what is the expedient definition of the biological species, having regard to the aim of stability in concepts and nomenclature and to what is the most recognizable cut-off point between a species and a not-yet-species.

Nomenclature

Further modifications have been made to the second edition of the *International Code of Zoological Nomenclature* and a third edition is in the course of preparation. The principal change involves the contentious and ambiguous Article 23(b), the purpose of which was to prevent, by an automatic provision of the Code, the upsetting of established nomenclature through the bringing into use of long-forgotten names under the Law of Priority. Under decisions approved by the XVIIth International Congress of Zoology (see *Bull. zool. Nom.* 29: 185–6), this purpose is now achieved by appropriate amendments to Articles 23, 79 and 80. The effect of these is to require a zoologist who considers that the application of the law may in a particular case disturb stability or universality, or cause confusion, to maintain 'existing' (i.e. the most common) usage and refer the case to the International Commission for decision. For the guidance of both working zoologists and the Commission, criteria are provided in Article 79 for judging whether stability would be threatened by the reintroduction of a forgotten name that is a senior synonym of a name in general use.

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EVOLUTION AND CLASSIFICATION OF THE INSECTS

by I. M. MACKERRAS

Ancestry of the Insects

Two major contributions to the solution of this problem have appeared. In the first, Manton (1972) has extended and integrated her previous studies (pp. 154–5) of the comparative functional morphology of limbs and jaws, and crystallized her conclusions in the following formal classification of phylum, subphyla and classes.

UNIRAMIA		
ONYCHOPHORA	MYRIAPODA	HEXAPODA
	Diplopoda	Protura
	Pauropoda	Diplura
	Chilopoda	Collembola
	Symphyla	Thysanura
		Pterygota

She stressed the independence of the hexapod classes, dismissing the former Entognatha (pp. 155–6) as a convergent assemblage—a conclusion with which Tuxen (1970) would not agree—and the Ectognatha (= Insecta) on the grounds that ‘there can be no common ancestry which particularly links the Thysanura [= Apterygota of this book] and Pterygota, because the five hexapod groups possess mutually exclusive leg mechanisms, although sharing the same basic type of jaw mechanism which contrasts with all myriapods.’

In the second publication, Anderson (1973) has integrated extensive comparative studies of annelid and arthropod embryology, with particular emphasis on patterns of cleavage, cell lineages and fate maps of the blastoderm. Like Manton, he has sought at every point for evidence of functional and anatomical continuity, for the compatible and the mutually exclusive in evolutionary logistics. His synthesis has provided substantial support for the thesis that Crustacea, Chelicerata and Uniramia are separate, independent phyla, that the Uniramia are a

monophyletic assemblage, and that they, alone of the three, shared a remote common ancestry with clitellate annelids. He also agrees with Manton on the relationships of the subphyla, and that ‘an early divergence must have occurred between the ancestors of the Diplura, Collembola and Thysanura [= Apterygota] probably before any of them had attained the hexapod state’, but differs in concluding that ‘there seems little doubt, however, that the ancestors of the Pterygota were hexapodous relatives of the Thysanura.’

This last conclusion is supported, also on embryological grounds, by Jura (in Counce and Waddington, 1972) and by many apparent evolutionary continuities between Apterygota and Pterygota in post-embryonic morphology, including that of the terminal abdominal segments and their appendages (pp. 20–8) and of the thysanuran-like larvae of Ephemeroptera.* It does not seem impossible that mutually exclusive patterns may arise from an ancestral plan that differs from both.

Evolution of the Pterygota

Wigglesworth (1973b) has put forward a new theory that wings did not evolve from paranotal lobes (or from branchial lamellae), but from coxal styles on the thoracic legs which had developed into gill-plates in secondarily aquatic apterygotes. Like the theory of Riek (1971a; and in Peters and Peters, 1973, pp. 176–7) that the ancestral insects were primarily aquatic, this line of reasoning would lead rather directly to the Ephemeroptera as representing the first of the pterygotes.

Beier and Hennig, as noted on p. 28, have removed the Plecoptera from the blattoid-

* See also Birket-Smith (1974).

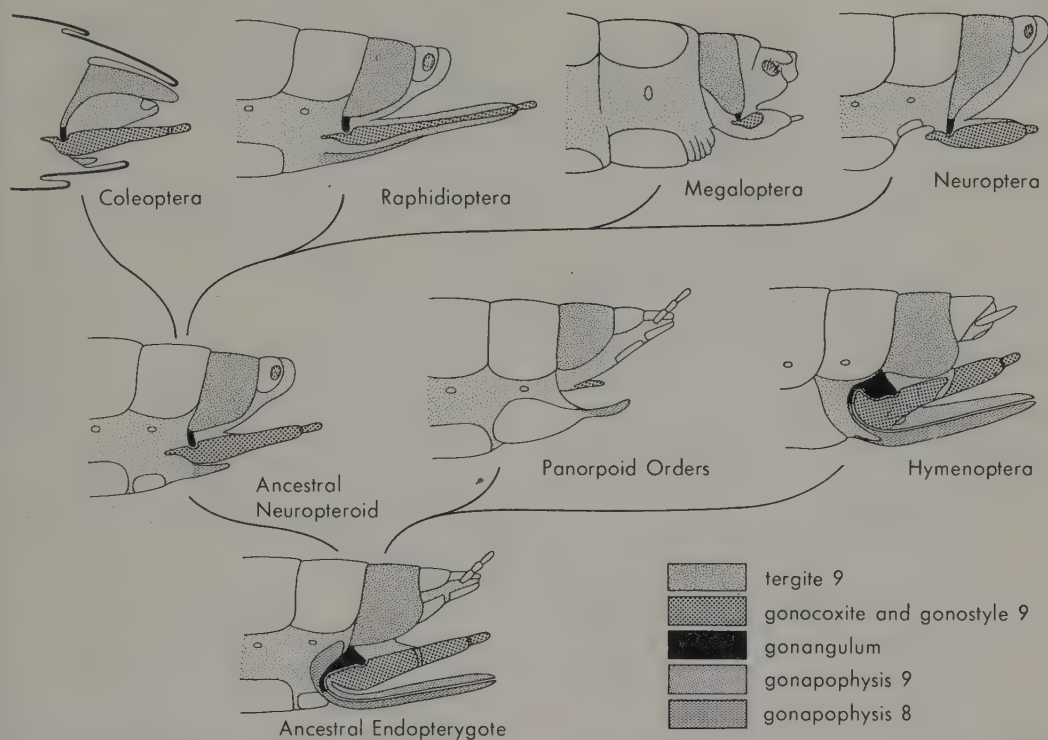


Fig. 11. Evolutionary pattern of the endopterygote orders as indicated by the female terminalia (after Mickoleit, 1973).

orthopteroid orders, and M. White (1971) would be inclined on cytological grounds to remove the Dermaptera also. The trend here seems to be towards a multiplicity of superorders. In contrast, and in spite of Rasnitsyn's (1969) opinion that the Hymenoptera had a completely separate origin, there appears to have been only one primary division in the endopterygotes, into a neuropteroid-coleopteroid line on the one side and a

panorpoidea-hymenopteroid line on the other. It is clearly indicated in Malyshev's (1968) review of the ancestry of Hymenoptera, in Mickoleit's (1973) study of the female terminalia (Fig. 11), and in unpublished studies of the male terminalia by the present author. It would seem that two superorders, Neuropteroida and Panorpoidea, rather than four (or possibly more) would provide the clearest picture of relationships.

FOSSIL HISTORY

by E. F. RIEK

The Fossil Record

A species of Palaeodictyoptera with some features of the Megasecoptera has been recorded from Upper Carboniferous shales in Tasmania by Riek (1973b). This is the oldest insect fossil known from the southern hemisphere, and it apparently lived in an unusually cold climate, for it was found in sediment at the margin of a lake associated with glacial moraines.

An interpretation of the environment of the Lower Cretaceous freshwater beds in Victoria (p. 171) has been presented by Waldman (1973). Two fleas have been recorded by Riek (1970c). One is a modern type, whereas the other, although with specialized leg structure, retains the plesiomorphic characters of nematocerous-like antennae and non-jumping hind legs.

History of the Orders

ARCHAEOPTERA. *Eopterus* and *Eopteridium* have been found to be part of the tail-fan of eumalacostracan Crustacea (Riek, in Hamilton, 1971, p. 425n.; Rohdendorf, 1972), so the evolution of Palaeoptera and Neoptera from an ancestral 'archaeopteron' (Rohdendorf, 1969) cannot be sustained.

PALAEOPTERA. Recent studies (e.g. Kukalová, 1970, 1973) strengthen the view that the Palaeodictyoptera and Megasecoptera, and also the Diaphanopterodea, form a related complex of orders distinguished by their haustellate mouth-parts and other specializations, including projections from the terga of thorax and abdomen. The immature stages, at least of Palaeodictyoptera, were also haustellate (Sharov, 1971) and appear to have been terrestrial, in contrast with the Odonata and Ephemeroptera with which there are nevertheless indications of relationship in the adult terminalia. The

structure of the mouth-parts precludes this group of orders from the ancestry of Neoptera, other possibly than the hemipteroid orders as proposed by Rohdendorf (1969). There is, however, little morphological evidence to support Rohdendorf's hypothesis and it seems more likely that the Neoptera were monophyletic, though their palaeopterous ancestors have still to be discovered.

NEOPTERA. A consensus is also appearing (e.g. Hennig, 1969c; Beier, 1969; Hamilton, 1972) to set the Plecoptera and their relatives apart from other Polyneoptera (blattoid-orthopteroid orders), or even to remove them from the Polyneoptera altogether (Beier, Hennig). The relevant part of Table 8.1 (p. 169) should therefore be replaced by the arrangement set out below.

PLECOPTEROIDEA	ORTHOPTEROIDEA
Paraplecoptera (Carb.-Trias.)	Protorthoptera (Carb.-Trias.)
Plecoptera (Perm.-Recent)	Orthoptera (Carb.-Recent)
Miomoptera (Perm.)	Phasmatodea (Trias.-Recent)
Embioptera (Perm.-Recent)	Caloneuroidea (Carb.-Perm.)
Zoraptera (Recent)	Glosselytroidea (Perm.-Juras.)
	Protelytroptera (Perm.)
BLATTOIDEA	Dermaptera (Juras.-Recent)
Blattodea (Carb.-Recent)	Grylloblattodea (Recent)
Isoptera (Eocene-Recent)	
Mantodea (Eocene-Recent)	

Among the orthopteroids, inclusion of the saltatorial Oedischiidae in the Orthoptera extends the time range of that order back to the Upper Carboniferous, while Caelifera and Phasmatodea are now known from the Lower Triassic of Russia (Sharov, 1968). Kukalová (1966) recorded additional Protelytroptera from the Upper Permian of

Australia. In the endopterygotes, Raphidiop-
tera have been recognized in the Upper
Carboniferous (Smart and Wootton, 1967;
Rohdendorf, 1969) and further study has
convinced the writer that Tillyard was correct
in including the Upper Carboniferous *Metro-*
pator in the Mecoptera. Thus, in spite of the
doubts expressed by Hennig and F. M. Car-

penter, there is reason to believe that
endopterygote insects were well established
before the beginning of the Permian when
their first major radiation began. The
Permian Platychoristidae and Permomerop-
idae were wrongly included in the Trichop-
tera on p. 185, but are now returned to the
Mecoptera (*sens. lat.*).

9

COMPOSITION AND DISTRIBUTION OF THE FAUNA

by I. M. MACKERRAS

Recent additions to the known Australian
fauna have not materially affected the
account given on pp. 191-7. A possible
exception may be an intensive, but still in-
completely studied, survey of Arnhem Land
in the Northern Territory (CSIRO, 1973),
some results of which are referred to in later
chapters. Gressitt (1974) has published a
comprehensive modern review of insect bio-
geography.

Plate Tectonics

The term had been coined by 1968, but
was not mentioned in the original chapter;
now it is the central concept unifying the
whole of palaeogeography. The outer crust of
the earth (lithosphere) is divided into seven
or eight huge plates and some smaller frag-
ments (microcontinents), which are formed
by upwelling from the mantle at rifts (mid-
ocean ridges), consumed at island arc-trench
systems, and move past one another at mega-
shears, carrying the lighter land masses
passively with them. The reality of the con-
cept has been supported by a great deal of
new evidence, including many detailed
patterns of magnetic reversal, and by the way

it has accounted for a variety of observed
phenomena, such as mountain building and
the patterns of earthquake epicentres.

These events and the associated move-
ments of the continents have been reviewed
and documented by Dietz and Holden
(1970), Vine (1970), Cracraft (1973) and, at
a more general level, by Dewey (1972),
McKenzie and Sclater (1973) and in Talbot
(1972). The summary of southern palaeo-
geographic history below is based mainly on
the reconstructions of Dietz and Holden as
modified by Cracraft's later analysis of the
literature.

The upper end of the time scale has been
revised since Table 8.1 (p. 169) was pre-
pared, the following figures, in million years
(m.y.) since the beginning of the periods,
being representative (Doutch, in Walker,
1972).

Holocene	0-010	Miocene	22.5	Palaeocene	65
Pleistocene	2	Oligocene	36	Cretaceous	136
Pliocene	5.5	Eocene	53.5	Jurassic	195

Separation of north-western Africa from
North America was completed about 180
m.y. ago, freeing Gondwana from Laurasia
except for a point of contact with Spain.

Gondwana then broke up in approximately the following sequence.

Africa from Antarctica: between 170 and 100 m.y. ago (uncertain).

South America from Africa: progressively from 130 m.y. in south to 80 m.y. in north.

India from Africa (or Australia): drift began *ca* 100 m.y., ceased at 45 m.y., resumed at 36 m.y., completed between 20 and 10 m.y.

South America from Antarctica: a complex area, with E. Antarctica originating separately from W. Antarctica and with microcontinents and island arcs in the Scotia Sea; 'continuous land might have existed off and on throughout the Mesozoic and early Cenozoic' (Cracraft).

Australia from Antarctica: drift began at 45–43 m.y., completed between 15 and 10 m.y.

New Zealand: separated from Antarctica at 80 m.y. (Cracraft); central Tasman Sea formed by sea-floor spreading from 80 to 60 m.y. only, and southern Tasman Sea formed by separation of Australia from Antarctica at *ca* 50 m.y. (Hayes and Ringis, 1973).

Palaeoclimatology, of vital importance in biogeography, is too large a subject to discuss here. Cracraft (1973, pp. 481–9) has reviewed the Cretaceous and Tertiary regional climates, mainly as indicated by palaeobotanical analysis, Marks (1972) the Tertiary climates of Queensland, and Jessup and Norris (1971) the evolution of aridity in the Lake Eyre basin.

Some Biological Implications

The most fundamental implication to the biologist is that, if one defines systematics as the study of the evolution of taxa in time and space, as many do, then the relevant findings of modern plate tectonics must be regarded as an integral part of systematics. If one's reconstruction of phylogeny is inconsistent with those findings, the inference should be that it is probably wrong. This reverses a principle (pp. 188–9) of many years' standing, but biogeographical evidence is no longer relevant to palaeogeography, except

as an aid in dating the times of events and as a guide to palaeoclimates.

A second, more specific implication is the attention that should be directed to the Cretaceous as the time when many family- and genus-group taxa evolved in the southern continents. This is supported not only by patterns of distribution but by recent palaeontological findings, such as those of Wilson *et al.* (1967) on ants, H. Evans (1969a) on aculeate Hymenoptera, MacKay (1970) on Lepidoptera, and J. McAlpine (1972) on Diptera, all in America, and the largely unpublished findings of Riek (p. 171) in Victoria.

A third, of special local interest, is the manifest importance of island arc-trench systems as pathways of dispersal. The series leading from south-eastern Asia into the Pacific is shown in Figure 12, in which the spots indicating earthquake epicentres could have served as readily to mark the distributions of many insect groups. Formation of trenches must coincide with commencement of drift, but it doubtless takes time for islands to build up sufficiently to serve as stepping-stones. To judge from the maps used by Douth (in Walker, 1972, Fig. 1.1), those north of New Guinea would have been operational for reasonably good travellers at least 20 m.y. ago. It is more difficult to estimate when a land mass, such as Australia

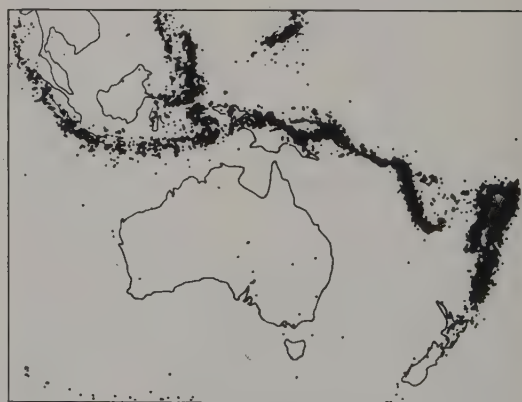


Fig. 12. Pattern of earthquake epicentres marking the island arc-trench systems between Asia and the Pacific (after Vine, 1970).

plus southern New Guinea, approaches near enough to an arc-trench to come under its biogeographical influence, and the difficulty is increased by the fact that continental margins are often at a considerable distance from the coast lines. The onset of rapid mountain building as piling up and buckling of the land occurs (*ca* 10 to 15 m.y. ago in northern New Guinea) may give a fair approximation. Actually, it seems likely that the first effective biogeographical contact of Australia was with Timor at a slightly earlier date.

The Oriental Region

This is a particularly interesting area which was treated too cursorily on p. 191. It is the only region that is structurally composite, in that it consists of a northern strip

that was continuous with Laurasia, a series of island arc-trench systems to the south and east of Laurasia (those to the east forming Wallacea), and India, a Gondwana fragment that joined the complex in the Miocene. The earlier statement erred in underestimating the contribution that Africa has made, both of older Gondwana and more recently evolved elements, to the Oriental fauna. It has been documented, for example, for Ephemeroptera by Peters and Edmunds (1970), for Embioptera by E. Ross (1970), for Trichoptera by H. Ross (1967), and is noted in several chapters in the present work. The principal pathway was presumably the one that existed between Africa-Arabia and Asia from the closure of the Tethys Sea in the Cretaceous to the onset of aridity in the Miocene.

10

THE ENTOGNATHOUS HEXAPODS

by M. M. H. WALLACE

General works on embryology by Jura (in Counce and Waddington, 1972) and Anderson (1973), on functional morphology by Manton (1972), and on the relationships of the classes by Tuxen (1970) are reviewed on p. 26, though it may be noted here that the embryology of Protura still remains unknown. In the Diplura, Pagés (1972) proposed to raise the Heterojapyginae to family rank in Japygoidea, and Townsend (1970) has described and illustrated the egg clusters of *Heterojapyx novaezeelandiae* (Verh.) from New Zealand. No new Australian Diplura have been reported, but S. L. Tuxen (personal communication) has an undescribed species of *Berberentulus* (Protura).

Class COLLEMBOLA

Butcher *et al.* (1971) have reviewed the

literature on the ecology of edaphic Collembola. A study of the secondary sexual characters of the Symphypleona by Massoud and Betsch (1972) has particular relevance to the Australian fauna, in which specialized antennae occur in Bourletiellinae and Sminthuridinae.

Folsomides deserticola Wood (**Isotomidae**) is widely distributed in arid and semi-arid soils of south-eastern Australia where it comprises 50–90 per cent of the total Collembola population at those sites. High densities (over 1,000/m²) are often attained during the hot dry summer months (Wood, 1971).

In **Sminthuridae**, two new genera, *Pygicornides* (Sminthuridinae) and *Bourletides* (Bourletiellinae), from the central coast of Western Australia have been defined by

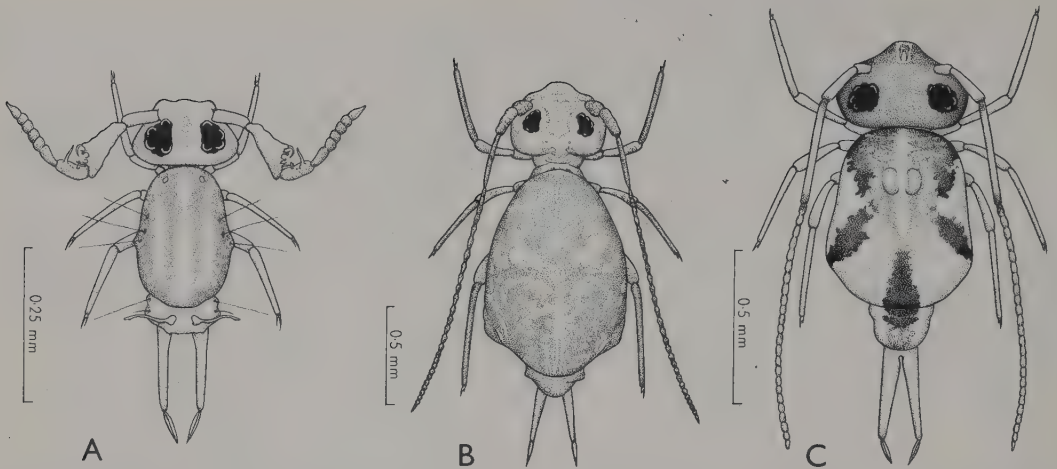


Fig. 13. Sminthuridae: A, *Pygicornides torridus*, ♂; B, *Temeritas denisi*, ♂; C, *Naosminthurus nigradorsalis*, ♂. [B. Rankin]

Betsch and Massoud (1972); both are characterized by secondary sexual dimorphism in the male antennae. *Pygicornides*, in addition, has two remarkable elongated appendages dorsally on the small abdomen (Fig. 13A). The genus *Temeritas* (W. Richards, 1968) with long antennae (Fig. 13B) is represented by two species in south-eastern Australia and one in south-western Australia; all were formerly included in *Sminthurus*. *Naosminthurus* (Fig. 13C), notable for the complex nasal organ in the male (Fig. 14), is known from a single species collected in south-western Australia. One of the commonest genera in northern Australia is *Corynephoria*, represented by at least 10 undescribed species. Wallace and Mahon (1971) have given a detailed account of the Australian distribution of *Sminthurus viridis* (L.).

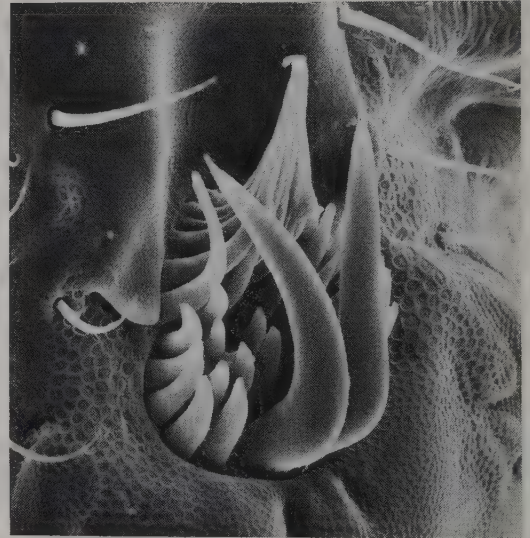


Fig. 14. Nasal organ of *N. nigradorsalis*, ♂, $\times 1000$. [Scanning electron micrograph by B. K. Filshie]

APTERYGOTA

(*Primitively wingless insects*)

by J. A. L. WATSON

Little further has been published on the Apterygota. Jura (in Counce and Waddington, 1972) has reviewed the embryonic development of the apterygote orders and stressed the affinities between Thysanura and Pterygota.* *Lepismodes inquilinus* and *Ctenolepisma longicaudata* absorb water

* Birket-Smith (1974) has now studied the abdominal morphology of apterygotes in detail, and concluded that the Archaeognatha are closer to the pterygotes.

from subsaturated atmospheres down to 45–60 per cent relative humidity through the highly convoluted rectal wall, unlike *Machiloides* and other Archaeognatha which take up water from liquid films through the exsertile vesicles (Noble-Nesbitt, 1970; E. Smith, 1970; Noirot and Noirot-Timotheé, 1971b). Paclt (1967) listed 16 species of lepismatids known from Australia, and Watson and Li (1967) keyed the domestic species.

EPHEMEROPTERA

(*Mayflies*)

by E. F. RIEK

Illies (1968) has given a general account of the order, but the most notable recent event was the First International Conference on Ephemeroptera held in Florida in 1970 (Peters and Peters, 1973), at which papers were presented on comparative morphology, life histories, ecology, distribution, and in an extensive symposium on classification. Some publications that have appeared since the Conference are noted below. There have been no additions to the described Australian fauna.

Phoresis and Parasitism

Arvy and Peters (in Peters and Peters, 1973) reviewed the parasites and commen-

sals of mayfly nymphs, including parasitism by chironomid and phoresis by simuliid larvae and pupae, and Burton and McRae (1972) have added information on Simuliidae. Phoretic Simuliidae have not as yet been encountered in Australia, but tube-dwelling chironomid larvae and their pupae (*Symbiocladius* sp.) have been found attached to nymphs of *Atalonella* and *Atalophlebioides* (Leptophlebiidae) in cool mountain streams (Fig. 15). When fully grown they are almost as large as the host nymphs.

Biogeography

Although the higher classification of the order is still unsettled, there are a number

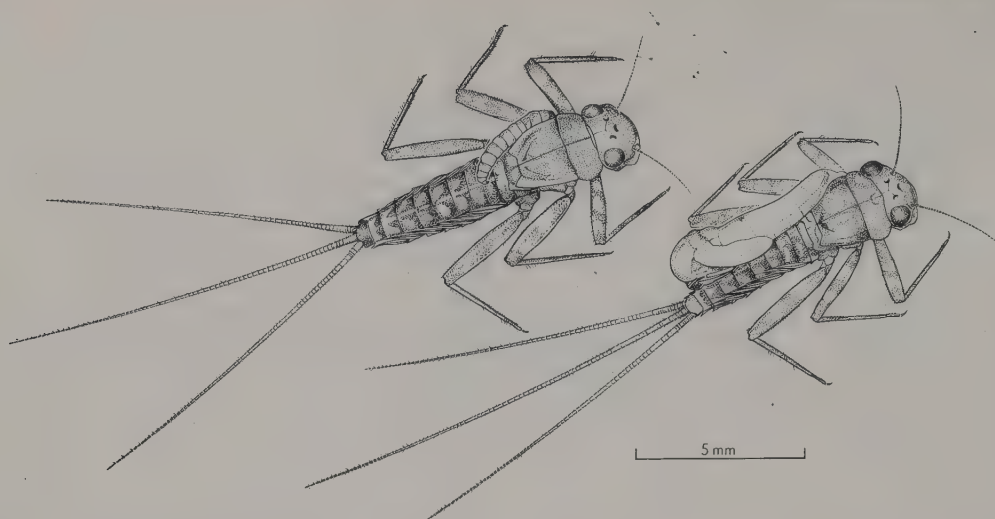


Fig. 15. Parasitic larva and pupa of *Symbiocladus* sp., Chironomidae, on nymphs of *Atalophlebioides* sp. Young larvae face in the same direction as the nymph, but older larvae and pupae always face backwards. [S. Monteith]

of clearly defined phyletic lines and G. Edmunds (1972) has analysed their distributions. Trans-Antarctic relationships are strong, being shown by Siphonuridae-Ameletopsinae, the *Metamonius* group of genera, Coloburiscinae and Oniscogastrinae, and many Leptophlebiidae, all of which are found in Chile, southern Australia and New Zealand. One group of leptophlebiid genera occurs also in southern Africa (Peters and Edmunds, 1972). The only mayflies known from New Caledonia are Leptophlebiidae related to those from New Zealand.

A second, very strong, Ethiopian-Oriental element (the 'Ethiopian-Oriental arc' of Edmunds), with evidence of Neotropical relationships to the west and Holarctic relationships to the north, extends around the Indian Ocean to New Guinea and Australia. Its Australian representatives include many of our Baetidae, our only ephemerellid, and all our Caenidae, whilst Ethiopian-Oriental Leptophlebiidae (*Masharikella*, *Choroterpes* and a related genus) have been discovered recently over a wide area of extreme northern Australia. Prosopistomatidae extend to New Guinea, but have not yet been found in Australia.

Classification

The various schemes of classification discussed in Peters and Peters (1973) were based broadly on characters of adults and nymphs (Edmunds) or primarily, though not exclusively, on eggs (Koss; see also Koss, 1968), the tracheal system, Malpighian tubes and nerve cord of nymphs (Landa), the 'gill' appendages, body form and cerci of the nymphs and venation of the adults (Riek), or, at the generic level in Leptophlebiidae, on thoracic morphology of adults (Tsui; Tsui and Peters, 1972). A new classification of both fossil and Recent mayflies has been published by Tshernova (1970). All the schemes agree in treating the Siphonuridae as the most primitive surviving mayflies and (with Demoulin, 1969) the Baetidae as having been derived from Siphonurinae. They differ chiefly in the number of superfamilies recognized (5 to 7, mostly 6) and in the allocation of families to particular superfamilies, but agreement on family relationships appears to be developing. The classification proposed by the writer differs from that on p. 231 mainly in separating Caenoidea from Ephemeroidea, and Siphonuridae from Baetidae.

ODONATA

(Dragonflies and damselflies)

by A. F. O'FARRELL and J. A. L. WATSON

A specialist journal, *Odonatologica*, has been published since 1972 by the International Society of Odonatologists. Cytotaxonomic studies of Odonata are now developing (e.g. Kiauta, 1972), but little is as yet known about Australian forms.

Physiological Colour Change

Physiological colour change has been reported in 10 genera of 6 families (Aeshnidae, Amphipterygidae, Coenagrionidae, Lestidae, Megapodagrionidae, Libellulidae). Minute refractive bodies in the distal cytoplasm of epidermal chromatophores produce Tyndall scattering of light, against a dark background of ommochrome-laden vesicles in the proximal cytoplasm, usually giving intense blue colour, stable at higher temperatures (e.g. 20–25°C) but replaced by dull purplish-grey or black when distal migration of ommochrome vesicles disrupts this optical system, e.g. at 10–16°C (O'Farrell, 1971a). Suitable adjustment of ambient temperature and light intensity may induce several successive cycles of colour change in isolated integument *in vitro*, but central control mechanisms may also be involved (Veron, 1973b).

Various thermoregulatory functions may be ascribed to the dark colour phase (O'Farrell, 1971a), but adaptive functions of the bright colouring remain obscure, as do those of colour changes restricted to small areas of the body, e.g. in *Aeshna brevistyla* and *Argiolestes alpinus*.

Population Studies and Age Estimation

Mark-recapture methods are useful in population studies on adults, if they are weak fliers uninjured by capture and show behaviour predictable enough for effective

sampling (Waage, 1972). Stronger fliers may be marked and counted while roosting at night, but specialized roosting behaviour (O'Farrell, 1971b) may make random sampling difficult. Age distribution may be estimated on the basis of known *morphological* colour change (Parr and Palmer, 1971) if *physiological* colour changes do not complicate this situation (Bick and Bick, 1965). Examination of gonads (C. Johnson, 1973) or daily growth layers of endocuticle (Veron, 1973a) are laboratory methods of ageing adults. Veron's method may be unworkable very early or late in the adult life span.

Classification and Distribution

The known Australian species and subspecies of Odonata have been increased from 248 (p. 253) to 283, most of the additions being from northern Australia. The additions include 10 protoneurids, 1 lestoideid, 4 coenagrionids, 1 megapodagrionid, 2 lestids, 1 chlorolestid, 8 gomphids, 2 aeshnids, 6 corduliids, and 7 libellulids (Watson, 1969, 1974; Watson, in CSIRO, 1973). These and new distributional data have rendered Fraser's keys unworkable for many species and genera. The distributions are given in Table 1. The richest regional faunas are those of the east and north, but documentation of the dragonflies of Tasmania, Cape York and the Kimberleys is poor.

The main tropical groups are the protoneurids, coenagrionids, anactine and gyna-canthagine aeshnids, and libellulids, whereas the megapodagrionids, neopetaliine and brachytronine aeshnids, and synthemids are overwhelmingly Bassian (p. 196). The gomphids are widely spread in Australia, but almost all species show affinity with South

American gomphids and, together with the Chlorolestidae, Petaluridae, Neopetaliinae and possibly gomphomacromiine Corduliidae, suggest derivation from an ancient Gondwana fauna.

The following characters will correct and supplement the key to nymphs of Zygoptera on p. 255.

Protoneuridae-Protoneurinae: gills denodate or subnodate; ligula entire; at most one pair of mental setae.

Amphipterygidae: outer border of labial palp

with row of short stout setae; **Lestoideidae** with basal tuft of long setae.

Megapodagrionidae: gills sometimes swollen, triquetral, nodate, with long terminal filament; mental setae absent.

Lestidae: end hook of labial palp bearing setae.

Chlorolestidae: mental and palpal setae absent; ligula deeply cleft.

Coenagrionidae: gills weakly nodate or denodate; ligula entire; more than two pairs of mental setae.

Protoneuridae-Isostictinae: gills strongly nodate, constricted at node; ligula shallowly cleft; not more than two pairs of mental setae.

TABLE 1
Numbers of Species of Australian Odonata, by Regions

Families	TOTALS	S-W W.A.	S-E S.A.	VICTORIA	TASMANIA	E N.S.W.	S-E QD	N-E QD	CAPE YORK	N N.T. KIMBERLEYS	N-W W.A.	INLAND	EXTRALIMITAL
ZYGOPTERA	97												
Protoneuridae	22	—	1	4	—	4	6	8	6	12	2	4	—
Lestoideidae	2	—	—	—	—	—	—	2	—	—	—	—	—
Coenagrionidae	30	4	5	7	5	14	16	21	16	18	8	7	13
Megapodagrionidae	15	4	—	3	—	6	5	5	—	1	—	—	2
Lestidae	13	5	5	6	6	6	3	6	5	4	2	3	2
Chlorolestidae	8	—	—	2	—	4	2	4	—	—	—	—	—
Hemiphlebiidae	1	—	—	1	—	—	—	—	—	—	—	—	—
Amphipterygidae	4	—	—	2	—	3	3	2	1	—	—	—	—
Chlorocyphidae	1	—	—	—	—	—	—	—	1	—	—	—	1
Calopterygidae	1	—	—	—	—	—	—	—	1	—	—	—	1
ANISOPTERA	166												
Petaluridae	30	3	5	6	1	9	12	15	7	8	4	3	—
Gomphidae	4	1	—	—	—	1	1	2	2	—	—	—	—
Aeshnidae— Neopetaliinae, Brachytroninae, Aeshninae	27	2	3	13	6	16	9	8	1	—	1	1	1
Aeshnidae—Anactinae, Gynacanthaginae	9	2	1	1	—	2	3	6	7	7	2	2	7
Synthemidae	15	4	2	6	3	8	6	4	2	—	—	—	—
Corduliidae	30	5	2	5	2	13	10	12	8	5	2	2	1
Libellulidae	51	9	7	7	2	21	31	39	37	36	13	14	38
Total species	263	39	31	63	25	107	107	134	94	91	34	36	66

BLATTODEA

(Cockroaches)

by the late M. JOSEPHINE MACKERRAS

Roth (1970) has reviewed the evolution of reproductive mechanisms in cockroaches and shown that they support the McKittrick system of classification used in the main volume. Further support from independent structures has been provided by studies of the Malpighian tubes (Leconte *et al.*, 1967) and spermatophores (Graves, 1969). A. Richards (1971a) has recorded the obligate troglobite *Trogloblattella nullarborensis* Mackerras (p. 266) and five facultative troglaphiles—*Polyzosteria mitchelli* (Angas), *P. pubescens* Tepp. and *Zonioploca medilinea* (Tepp.) (Blattidae), *Gislenia fulva*

(Sauss.) and *Paratemnopteryx rufa* (Tepp.) (Blattellidae)—from caves in the Nullarbor Plain, southern Australia. M. J. Mackerras (1968a–c) completed her revision of the Blattidae, defined a new genus and species of Blaberidae, and provided revisional notes (including 2 new genera and 3 new species) on Australian Polyphagidae. Roth and Princis (1973) have revised the genus *Calolampra* (Blaberidae), recognizing 26 species, of which 12 were new.

These notes were prepared by I. M. Mackerras with help from Mrs Helen Cameron and Miss Josephine Cardale.

ISOPTERA

(Termites)

by F. J. GAY and J. A. L. WATSON

Two modern texts on termites have been published—Krishna and Weesner (1969–70) on termite biology, and Lee and Wood (1971) on the interactions between termites and soils. Both works include considerable information on Australian termites.

Development and Polymorphism

Studies of the development of the immature stages have shown differences between the more primitive termites and the Termitidae (Noirot, Miller, in Krishna and Weesner, 1969; Watson, 1971). In primitive

termites (Mastotermitidae, Kalotermitidae, Termopsidae) the larvae undergo three or more moults before reaching the pseudergate stage. These pseudergates can moult without undergoing further differentiation, or can moult to the presoldier (white soldier), to a reproductive nymph with wing buds which develops through one or two further instars into the alate, or to replacement reproductives. In Termitidae, the first-instar larva moults either to a reproductive nymph, or to a second-stage larva which generally produces the first of up to five worker instars; the

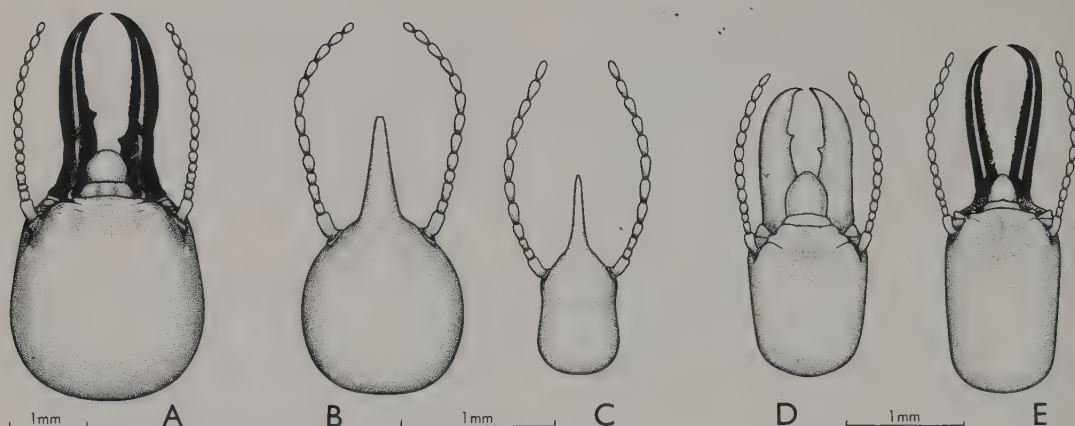


Fig. 16. Heads of: A, first soldier in incipient colony of *Mastotermes darwiniensis*; B, C, major and minor soldiers of *Tumulitermes recalvus*; D, E, presoldier and soldier of *Microcerotermes boreus*.

[B. Rankin]

presoldiers can arise from several of the worker instars. In some species there are large and small worker lines, the dimorphism involving a sexual component; these large and small workers produce major and minor presoldiers (and soldiers) respectively. Termitid reproductive nymphs moult five times before becoming adults, but can also produce replacement reproductives.

In incipient colonies the number of moults to the worker (or pseudergate) and soldier castes is commonly less than in mature colonies. The resulting small (nantic) soldiers may also differ in shape from those in established nests (Figs 15.10A, 16A).

Soldier polymorphism was noted (p. 290) as a characteristic feature of the genus *Schedorhinotermes*. In the *Nasutitermitinae*, soldier polymorphism is sporadic; it occurs frequently in *Tumulitermes*, occasionally in *Nasutitermes*, fairly commonly in *Occultitermes*, and rarely in *Occasitermes*. Polymorphism in this group of genera is generally restricted to differences in size, colour, antennal segmentation and, less commonly, in head shape, e.g. *Tumulitermes recalvus* (Hill) (Fig. 16B, C). The nantic soldiers produced in incipient colonies of polymorphic species are apparently minor forms. In *Nasutitermes* the major and minor soldiers show striking differences in defensive behaviour.

Both primary and secondary reproductives produce pheromones that affect caste composition in the colony. Disturbances in the pheromone or hormone production, or in other factors controlling caste determination, may result in the production of intercastes. Intercastes are now known between soldiers and adults, reproductive nymphs (Fig. 17), or workers; between presoldiers and neoteinics; and between workers and reproductive nymphs.

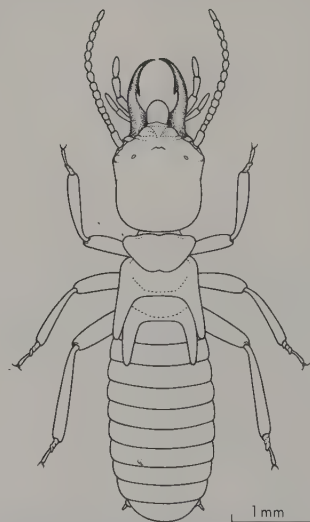


Fig. 17. Intercaste between soldier and reproductive nymph in *Amitermes xylophagus*.

[B. Rankin]

Termitophiles

Several termitophiles have been described recently. In the Staphylinidae, species of *Drepanoxenus* (Fig. 24) have been recorded with *Drepanotermes* (Kistner and Watson, 1972; Watson, 1973a); *Austrospirachtha*, a mimetic form (Fig. 25), occurs with *Nasutitermes* in the Northern Territory (Watson, 1973b). Species of *Pseudeba* (Tenebrionidae) feed on stores of forage in nests of *Drepanotermes* and *Nasutitermes* (Britton, 1973). Mitchell (1965) has described a termitophilous gecko from nests of *Nasutitermes triodiae* (Frogg.).

Termites and Soils

Lee and Wood (1971) have shown that the role of termites in Australian soils differs markedly from that of earthworms in temperate lands (p. 284). Starting from the premise that the principal effects of termites on soils are associated with their tunnelling and nest-building activities and their ability to decompose structural plant polysaccharides, they concluded that there was little evidence that gallery systems are ever extensive enough to have much effect on the porosity of the soil, although there is a tendency to invert soil profiles. Moreover, the chemically changed soils are largely concentrated in mounds and nests, where they are not readily available to soil micro-organisms. The organic residues from the degradation of plant material contain little of use to these micro-organisms and may depress their activity. On the other hand, there is little litter or accumulation of organic material in soils where termites are abundant, and termites commonly remove much dead material from grasses and herbage in arid areas, leading, in extreme cases, to denudation of pastures. This suggests that termites are important in recycling organic materials, particularly in drier ecosystems.

Systematics and Biology

Sands (1972) placed the Amitermitinae in synonymy with the Termitinae, reducing to 2 the subfamilies of Termitidae in Australia.

Close affinities among Australian genera involved (*Termes*, *Amitermes*, *Microcero-termes*) are indicated by the fact that the presoldiers of both *Termes* and *Microcero-termes* have a tooth about the mid-point of each mandible, which is absent in the soldiers (Fig. 16D, E), although it occurs in the soldier of *Amitermes* (Fig. 17).

The faunal count in 1970 was 182 species in 26 genera, the largest being *Amitermes* (Gay, 1968). The biology of many of these species was discussed by Gay and Calaby (in Krishna and Weesner, 1970). Extensive surveys, mainly in north-western and inland Australia, have since increased the known fauna to 246 species (51 undescribed) in 30 genera. Two new genera, *Hesperotermes* (1 sp.) and *Ekphysotermes* (4 spp.), have been erected for species previously assigned to *Termes* (Gay, 1971), and Australian species of *Procryptotermes* and *Incisitermes* have been discovered.

These surveys have also yielded information on the biology of various species, particularly of *Drepanotermes* (22 spp.) and *Tumulitermes* (47 spp.). These two endemic genera of harvesters are abundant in central and Western Australia. The species of *Drepanotermes* gather dry grass or leaf litter which is stored in subterranean nests or, more rarely, in mounds up to 1.5 m high (the 3 m nests noted on p. 291 were those of *Nasutitermes triodiae*). Colonies of *D. per-niger* (Frogg.) are relatively small, but can denude arid or semi-arid grasslands in the presence of sheep, and contribute to persistent disruption of the ecological balance (Watson *et al.*, 1973).

Although there have been many interceptions of exotic termites in Australia (Gay, in Krishna and Weesner, 1969), successful establishments are few. *Cryptotermes domesticus* (Havil.) and *C. dudleyi* Banks occur on Thursday Island, both infesting timber in buildings. Earlier reports of *C. dudleyi* in Darwin (p. 285) are almost certainly referable to a closely related native species, *C. secundus* (Hill), which is apparently confined to logs and trees. The cosmopolitan *C. brevis* (Walk.) has established itself in Queensland.

MANTODEA

(Praying mantids)

by K. H. L. KEY

Defensive Mechanisms

Advances have been made in the description and analysis of the defensive mechanisms of the Mantodea. M. Edmunds (1972), following Robinson (1969), distinguished between *primary* defensive adaptations, including crypsis, aposematic patterns, and mimicry, which reduce the probability of a vertebrate predator initiating an attack, and *secondary* defensive adaptations, such as escape, startle display, flash coloration, chemical defence, and thanatosis, which only operate under attack or immediate threat of attack. He described these mechanisms for 25 species of Ghanaian Mantodea, and concluded, *inter alia*, that the conspicuous black or coloured markings on the inner face of the anterior coxae and femora form part of the startle display and are not involved in courtship. However, they probably also have a role in the display connected with the now established defence of territory (MacKinnon, 1970). There is a striking species-specificity in the character and location (on wings, abdomen, fore legs, mouth-parts, cerci, etc.) of the markings used in the startle display, as well as some variability within common species. Edmunds interpreted this variety as indicating that the display is largely bluff, which can succeed only if any one form of it is relatively rare.

Edmunds stated that the early instars of several species are ant mimics. An undescribed species of *Paraoxyphilinae* from northern Australia and New Guinea has a wingless ant-mimic female and a fully winged 'normal' male. The females closely resemble a large brown ant belonging to the *yorkana* group of the genus *Rhytidoponera* and run with this species along its foraging trails. It is not known whether the function of the

resemblance is to enable the mantid safely to prey upon the ants, or to confer protection against its own possible predators; certainly the ants disregard its presence. In general, it now seems likely that the cryptic resemblances of Mantodea are primarily self-protective (strictly procryptic) rather than devices for lulling prey into a false security (anticryptic), although the immobility of the predator must surely have this latter function.

Analysis of Predation

Holling (1963, 1966) has provided an elegant experimental analysis of predation in *Hierodula crassa* Giglio-Tos, as part of a general investigation of the 'invertebrate functional response' to prey density; supporting data were obtained for *Mantis religiosa* L. The work included a study of the functioning of the fore legs in the predatory attack and established a precise relationship between their dimensions and the experimentally determined optimal size of prey.

It was found that feeding in *H. crassa* was restricted to the daylight hours and that the light-established rhythm was then retained under continuous light. Hunger, defined as the weight of house flies required to satiate 'standard' females, rose with the period of food deprivation to a sustained maximum. No stalking or striking at prey could be elicited in less than 8 hours after satiation; the maximal distance over which a fly could induce stalking then increased nearly linearly with the hunger level, as did the maximal distance over which awareness of the prey was signalled by a turning of the mantid's head, although the latter was much greater than the former. The 'reactive field', which encompassed almost 360°, was longest directly in front of the insect and decreased in radius

backwards; binocular vision was achieved between about 50° and 310° , and the minimal visual angle increased with the angle to the body axis, from 1° to 4° . A mantid that has started stalking a given fly is not diverted by another nearer one; flies in flight are rarely struck at and still more rarely captured. Hunger had no significant effect on strike success, which averaged 0.63. The average velocity of stalk was *ca* 3.5 cm. min.⁻¹. The average strike distance was 1.54 cm in front of the head and the extreme 2.5 cm. The time taken to complete a meal was independent of hunger level and amounted to 0.76 hr/g of prey in *H. crassa* and 2.96

hr/g in the smaller *M. religiosa*. After each fly is eaten there may be a 'digestive pause', during which a new attack will not be made. Mantids hand-fed from hatching were as reactive as normal ones when first presented with moving flies, but their catching success improved with experience.

The Australian Fauna

The number of Australian species now stands at more than 130, of which nearly 100 are Mantidae. *Pseudomantis albofimbriata* (Stål) has been found to attach its oothecae to the underside of stones.

17

ZORAPTERA

by C. N. SMITHERS

There has been no new information bearing on the possibility that this order might occur in Australia.

18

GRYLLOBLATTODEA

by K. H. L. KEY

There has been no new information bearing on the possibility that this order might occur in Australia.

DERMAPTERA

(Earwigs)

by E. T. GILES

Economic Significance. The cosmopolitan *Nala lividipes* (Dufour) has twice been reported as a pest. Infestations in the black earths (particularly when the soil was covered by litter) of the South Burnett, Darling Downs and Lockyer Valley districts of southern Queensland have been described by Hargreaves (1970). There the earwigs feed most frequently on seeds and seedlings of maize, but occasionally on sorghum, beetroot and summer and winter cereals. Damage to maize seedlings by *N. lividipes* has also been recorded from Kununurra in north-western Australia (Anon., 1971). The species is not known as a pest in other countries, e.g. Japan (S. Sakai, personal communication).

Classification. Popham (1973) has repeated his proposal to remove the Hemi-

merina to a separate order, but there is substantial cytological and morphological evidence (M. White, 1971; Giles, 1974) that they belong with the other suborders in the Dermaptera. The rearrangement of the traditional classification of the order by Popham has been continued by Popham (1965, 1968) and Popham and Brindle (1966-9), but it is still preferred to retain the arrangement followed on pp. 311-13. Recent work by Giles and Webb (see below) has shown that the Australian 'subspecies' of the cosmopolitan *Labidura riparia* (Pallas) is sufficiently distinct in karyotype and morphology to be restored to specific rank as *L. truncata* Kirby. There have been no other additions to described Australian Dermaptera.

CYTOTAXONOMY OF AUSTRALIAN DERMAPTERA

by G. C. WEBB

In general, dermapteran chromosomes are relatively small and probably holocentric, which is in contrast with the other blattoid-orthopteroid orders which have large, monocentric chromosomes (p. 73). Spermatogonial and somatic divisions in all members of the order so far investigated show typical holocentric chromosomes in the opinion of most authors (refs in White, 1971; Giles and Webb, 1972, pl. I, figs B, M). There are few restraints on the fusion and dissociation of holocentric chromosomes, and this could account for the relatively wide range of chromosome numbers noted below. Earlier studies had led some authors to a theory of evolutionary polyploidy associated with the origin of multiple sex chromosomes (see Henderson, 1970). However, recent work by the writer on *Forficula auricularia* (Webb

and White, 1970) and on a wide range of Australian Dermaptera has seriously impaired the credibility of the polyploidy theory.

The chromosomes of the male of *Hemimerus bouvieri* Chopard are $2n=7$ ($2AA+X_1X_2Y$), whereas, those of *Arixenia esau* Jordan are $2n=60$ ($29AA+XY$) (White, 1971, 1972). Thus the two divergent suborders, Hemimerina and Arixeniina, have respectively the lowest and the highest chromosome counts yet found in the order.

Karyotypes of some Australian Forficulina are shown in Table 2. *Nala lividipes* in Australia may prove not to be conspecific with representatives in other parts of the world, for its karyotypes known elsewhere are $2n\sigma=37$ ($17AA+X_1X_2Y$) from Spain and $2n\sigma=40$ ($A^LA^L+18AA+XY$) from India.

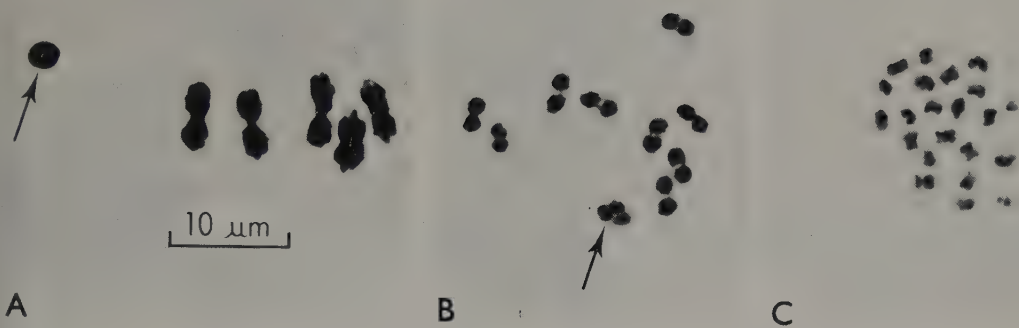


Fig. 18. A, *Dacnodes shortridgei*, first metaphase of ♂ meiosis, with 5 autosomal bivalents and the unpaired X chromosome (arrow); B, *Nesogaster erichsoni*, first metaphase of ♂ meiosis, with 9 autosomal bivalents and a sex trivalent, X₁X₂Y (arrow); C, *N. erichsoni*, ♀ mitotic metaphase from ovarian follicle epithelium (colcemid arrested). [Photos by G. C. Webb]

Labidura riparia (sens. lat.) may also not be a single species, for karyotypes with 2n♂ = 12 (5AA+XY) are known from Spain and 2n♂ = 14 (6AA+XY) from India and Japan, and the now separated *L. truncata* has the lowest number of chromosomes (all comparatively large) yet found in any forficuline (Giles and Webb, 1972). An unidentified species of rain-forest carcinophorine (not in the table) has the highest count of very small chromosomes with 2n♂ = 42 (19AA+X₁X₂X₃Y). *Chaetospania brunneri* (de Bor-

mans) has the greatest number of X-chromosomes yet found in the Dermaptera. Although *Dacnodes shortridgei* (Burr) has a relatively simple karyotype with XO males (Fig. 18A), another as yet unidentified member of the same primitive family has a karyotype 2n♂ = 20 (9AA+XY). *Nesogaster halli* Hincks, one of the relatively advanced Labiidae, also has XO males. There does not, therefore, appear to be any definite evolutionary trend in chromosome numbers within or between families of Dermaptera.

TABLE 2
Karyotypes of Australian Dermaptera
(Identifications by E. T. Giles)

	♂ karyotype	♀ diploid no.
PYGIDICRANIDAE		
<i>Dacnodes shortridgei</i>	11 (5AA+XO)	—
LABIDURIDAE		
<i>Euborellia annulipes</i> (Lucas)	24 (11AA+XY)	—
<i>Labidura truncata</i>	10 (4AA+XY)	10
<i>Nala lividipes</i>	34 (A ^L A ^L +15AA+XY)*	34
<i>Notolabis occidentalis</i> (Kirby)	24 (11AA+XY)	24
<i>Parisopsalis spryi</i>	32 (14AA+X ₁ X ₂ X ₃ Y)	34
LABIIDAE		
<i>Chaetospania brunneri</i>	31 (13AA+X ₁ X ₂ X ₃ X ₄ Y)	34
<i>Nesogaster erichsoni</i> (Dohrn)	21 (9AA+X ₁ X ₂ Y)	22
<i>Nesogaster halli</i>	19 (9AA+XO)	20

* A^L represents a distinctly larger autosome

PLECOPTERA

(Stoneflies)

by E. F. RIEK

Zwick (1973) has published a phylogenetic classification and catalogue of the Plecoptera, which he has divided into two newly based suborders on primary characters of the depressor muscles of the fore legs. Of the families known in Australia, the Notonemouridae—raised from subfamily rank in Nemouridae (Riek) or Capniidae (Weir, Illies)—belong to Zwick's Arctoperlaria and the other three (Eustheniidae, Austroperlidae, Gripopterygidae) to the Antarctoperlaria. All Australian Plecoptera have two small apical spurs on all tibiae, except Eustheniidae which have only one tibial spur on each leg, and nearly all except Notonemouridae have paired vasa deferentia and two separate gonopores. Nymphs of Austroperlidae may have either the simple anal gills illustrated in Figure 20.6B or the cerci and subanal plates beset with gills (Illies, 1969b).

All the Australian families are circum-Antarctic, being found in Australia, New Zealand and South America, with Notonemouridae also in South Africa and Madagascar (Zwick, 1973). The original record of an Australian gripopterygid from Fiji was apparently an error (McLellan, 1971). In

Australia, stoneflies occur predominantly in Tasmania and the south-eastern highlands with usual limits in southern Queensland, but the Gripopterygidae have been recorded also from South Australia and Western Australia and species of *Stenoperla*, *Trinotoperla* and *Dinotoperla* have been found recently in east-coastal streams of north Queensland.

The **Austroperlidae**, including 6 Australian genera, have been reviewed by Illies (1969b) and some of the known Australian **Gripopterygidae** (9 genera) by McLellan (1971). Illies (1969a) described a wingless gripopterygid from Victoria, Riek (1970a) the nymph of *Eunotoperla* from the south-eastern highlands, and Weir (1967) a new genus of **Notonemouridae** from southern Queensland. Riek (1973c) has published new keys to adults and nymphs of the Australian genera of Austroperlidae and proposed a new monotypic genus from eastern New South Wales.

While these notes were in press, H. B. N. Hynes (*Aust. J. Zool. Suppl.* 29: 1–52, 1974) published studies of the taxonomy of Austroperlidae and Gripopterygidae and on the eggs and biology of all four families.

ORTHOPTERA

(Grasshoppers, locusts, crickets)

by K. H. L. KEY

There has been so much recent work on this order that it will be necessary to restrict coverage very largely to its Australian members. Although accurate figures cannot be given, the number of Australian species now known—many of them undescribed—must be close to 2,000, about equally divided between the Ensifera and Caelifera. Of various proposals recently made for revising the family-group classification of the Caelifera, the only one that will be adopted here is the removal of the Eumastacidae and the South American Proscopiidae from the Acridoidea, to constitute a new superfamily Eumastacoidea. To accommodate this change, the first two couplets of the key on p. 339 should be modified as follows: couplet 1, line 1, delete 'ACRIDOIDEA'; couplet 2, line 3, insert 'EUMASTACOIDEA' before 'Eumastacidae'; line 5, insert 'ACRIDOIDEA' before '3'.

GRYLLACRIDOIDEA

The number of known Australian species now stands at approximately 160, the increase being largely due to a doubling of the number of **Rhaphidophoridae** as a result of a series of studies by A. Richards (e.g. 1971b). She has also published observations on the biology of some members of the group, including *Pallidotettix nullarborensis* Richards, a cave-frequenting species from the Nullarbor Plain (Richards, 1970). Mesa and his co-workers (see Mesa, 1970) have studied the chromosomes of several Australian raphidophorids; they find the basic karyotype of the Macropathinae to be $2n\sigma = 45$, with a metacentric X and XO males. In the **Stenopelmaticidae**, the first fully winged species, in an undescribed genus of Henicacinae, has been found in Queensland. In the

Gryllacrididae, a large species of *Hadrogryllacris* is preyed upon by *Sphex luctuosus* Smith.

TETTIGONIOIDEA

With the discovery of several new species of Tympanophorinae, as well as others distributed over several different subfamilies, the number of known species of Australian Tettigonioidea can now be provisionally set at about 320. A revision of the Decticinae being currently undertaken will undoubtedly add substantially to this total. Further study has shown that the two species of *Zaprochilus* previously reported should be referred to separate genera. The undescribed second genus is brachypterous in the male and apterous in the female and its tympana are poorly developed. It appears to be transitional to *Phasmodes ranatriliformis* Westw. The apterous male of the latter is now known; it has faintly indicated tympanal vestiges, although the female is correctly described as lacking tympana and this character has been used up to now to distinguish the subfamily Phasmodinae. A second undescribed genus of 'Zaprochilinae', obviously related to *Zaprochilus*, has the apices of the tegmina in the folded position curved upwards and sharply pointed. Densey Clyne (personal communication) has found that both it and *Zaprochilus* feed on the pollen and nectar of flowers, which probably explains the narrowly triangular, partly prognathous head of all four of these monotypic genera. In the light of the above findings, we should return to Caudell's (1912) concept of the subfamily Phasmodinae, which encompassed both *Phasmodes* and *Zaprochilus*.

Emsley *et al.* (1967) have considered the value of the stridulatory file and other

characters in tettigoniid taxonomy, while Bailey and Robinson (1971), following the elegant studies of Bailey (1970) and Bailey and Broughton (1970) on the mechanics of stridulation, have examined the probable role of the song as an isolating mechanism in the exotic genus *Homorocoryphus*. Karyotypes of Australian tettigoniids have been studied by White, Mesa and Mesa (1967), who found the listrosceline *Yorkiella picta* Carl to have XY males, and by Ferreira (1969), who reported 2 more XY species among some 11 examined, which included a probable pair of siblings in *Polichne*.

GRYLLOIDEA

The Australian members of this superfamily are being subjected to a comprehensive taxonomic revision which it is anticipated will bring the total of described species to nearly 700, including many siblings distinguishable by their songs (R. D. Alexander, personal communication). Lim *et al.* (1973) have examined the application of cytogenetics to taxonomy within the subfamily Gryllinae. The problem of the interrelations of the Australian *Teleogryllus commodus* (Walk.) and *T. oceanicus* (Le Guillou) and their races has been progressively elucidated by the cytogenetic and hybridization studies of Fontana and Hogan (1969) and Lim and his co-workers (see Lim, 1970), and by Hill *et al.* (1972), who established that the reproductive isolation of the two species in an extensive zone of overlap in south-eastern Queensland is achieved by the highly selective phonotactic responses of the females to the distinctive calling songs of the males. Hogan and Fontana (1973) have followed up earlier work by Hogan designed to make possible the genetic control of the injurious *T. commodus*, which has an egg diapause, by releasing a stabilized hybrid population of that species and *T. oceanicus*, which lacks diapause.

EUMASTACOIDEA

The **Eumastacidae** are credited by Blackith (1973) with a Gondwana origin, a conclusion that fits well with the fact that within this family the subfamily most closely related to

the endemic South American Proscopiidae is the endemic Australian Morabinae. M. White (1970) has described the karyotypes and meiotic mechanisms of representatives of several non-Australian subfamilies. The Australian fauna now numbers more than 250 known species. Key (1973) discussed the primary types of the 37 or 38 described species and their synonyms. Blackith and Blackith (1967, 1969b) have continued their series on the anatomy and physiology of the Morabinae with contributions on the muscles, nerves, tracheae and genitalia, and on proteins and pigments in solution; they have also discussed variation of anatomical characters (1969c) and the food of several different species (1966), and made observations on various other biological topics (1969a). Blackith (1967a) has bred from several different morabines the first hymenopteron to be recorded as a primary parasite of any grasshopper or locust, and described it under the name *Perilitus morabinarum* Blackith. He has also recorded (1967b) the tachinid fly *Myothyria fergusonii* Malloch as a common parasite of many morabines, as well as Acridoidea. White and his co-workers (references in White, 1973) have published numerous papers on the cytogenetics of the Morabinae, with special reference to the 'viatica group' and to the parthenogenetic species *Moraba virgo* Key and its relatives.

ACRIDOIDEA

The Australian Acridoidea (*sens. strict.*) now comprise at least 660 known species. With the removal of the Eumastacidae, only the Pyrgomorphidae and Acrididae remain. In the **Pyrgomorphidae**, Key (1969) has discussed the primary types of the 22 species he accepts as valid, together with their numerous synonyms. A distinctive new species of *Atractomorpha*, living on a single species of low, straggly shrub in Arnhem Land, brings to 3 the species of that genus, and of the tribe Atractomorphini, now known from Australia. The endemic tribe Psednurini has been revised by Key (1972), who recognizes 5 species in 3 genera; the unusual distributional relations of the 2 species of *Psednura*

were described by Key and Balderson (1972). In 1971 the most spectacularly colourful of all the Australian Acridoidea, *Petasida ephippigera* White, which had not been collected for about a hundred years, was rediscovered in Arnhem Land (Calaby and Key, 1973); an adequate coloured plate of this striking insect was published by Bolívar (1909).

The **Acrididae** have been the subject of an enormous amount of new work throughout the world. Many of the more important contributions will doubtless be cited in the forthcoming second volume of B. P. Uvarov's *Grasshoppers and Locusts* (in press). It will be possible here only to refer very briefly to some of the work on Australian species. Communicative aspects of reproductive behaviour in several Acridinae have been described by Otte (1972). Chromosomal studies have been carried out by Nankivell (1967) on *Austroicetes interioris* White & Key, and by Peacock (1970) on *Goniaea australasiae* (Leach); White (1968a) described a gynandromorph produced by double fertilization in *Valanga irregularis* (Walk.). The injurious *Phaulacridium vittatum* (Sjöst.) has been the subject of a comprehensive ecological study by Clark (1967) and of an earlier behavioural study by the same author cited therein; Jackson and

Cheung (1967) described a supernumerary chromosome with differential frequencies in males and females.

In the Australian plague locust, *Chortoicetes terminifera* (Walk.), papers have been published on the frequencies and inheritance of pattern morphs (see Byrne, 1967); on the protein and amino-acid content of the haemolymph in relation to diet and hydration (Djajakusumah and Miles, 1966; Muljadi, 1967); on egg development in relation to temperature and moisture (Wardhaugh, in Hemming and Taylor, 1972; see also p. 22); on flight, the factors initiating it, and its significance in dispersal and migration (Clark, 1969, 1971; Lambert, 1972); and on plague dynamics and field ecology (Clark, 1965, and in Hemming and Taylor, 1972, pp. 275-87; Clark *et al.*, 1969; Magor, 1970; Chinnick and Key, 1971).

TETRIGOIDEA

Several additional Australian species of the single family **Tetrigidae** have been discovered, including a very distinctive new genus from the sandstone plateaux of Arnhem Land. These bring the species total to about 80. The rain-forest species *Ving-selina brunneri* (Bol.) has been observed to ascend the trunks of trees to a height of ca 2 m from the forest floor after dark.

PHASMATODEA

(Stick-insects)

by K. H. L. KEY

General

A recent general account of the order is that of Beier (1968).

Defensive mechanisms have been discussed by Robinson (1969), who distinguished between *primary* and *secondary* defence (see also p. 40). Bedford and Chinnick (1966) described the secondary responses of the Australian *Eurycnema goliath* (Gray) and *Tropidoderus childrenii* (Gray), which may be elicited by sharply tapping the metasternum and basal abdominal sternites as the insect hangs from foliage. In *E. goliath* the wings are lifted to display the vivid red undersurfaces of the tegmen and the remigium of the hind wing, together with a pair of eye-like spots on the hind coxae. The widely spread hind legs are rapidly struck together, to the accompaniment of a swishing sound apparently involving the wings.

Bedford (1970) has described the embryology of *Didymuria violescens* (Leach), and Readshaw and Bedford (1971) have discussed embryogenesis in relation to parthenogenesis and diapause in the same species. Comparing several spatially separated populations, Readshaw and Bedford concluded that the capacity for parthenogenesis tends to be lost as that for diapause increases. Irrespective of the location of the populations, the optimal temperature for diapause development is ca 2°C, while embryogenesis proceeds more rapidly with rising temperature from a threshold of 7° up to 27°. Both processes can occur simultaneously at temperatures between the two optima. In the southern outbreak areas, highland populations experience two diapauses and the eggs overwinter at least twice before hatching; foothill populations experience only one diapause and the

eggs may overwinter either once or twice, depending on when they were laid. This is connected with the fact that a particularly cool summer appears to initiate the well known two-year abundance cycle. Readshaw (1968) earlier concluded, from a study of the seasonal movements and abundance of the pied currawong, *Strepera graculina*, that outbreaks of *D. violescens* are partly the result also of progressive relaxation of predation by this bird.

Craddock (1972, and in White, 1974a, pp. 24–42) has studied the karyotypes of 24 Australian species of Podacanthinae, Phasmatinae, Necrosiinae, Lonchodinae, and Pachymorphinae. She found male diploid chromosome numbers ranging from 26 to 45, with XO and XY sex-chromosome mechanisms. Five species have different chromosome-number races, a phenomenon not previously recorded for the Phasmatodea. *Didymuria violescens* has at least 10 such races, with chromosome numbers ranging from 26 to 40, and *Ctenomorpha chronus* (Gray) at least 3. In *D. violescens* the races come into parapatric contact, and in some cases hybrids have been found in the tension zones (see pp. 16, 25). This, together with laboratory crossing experiments, indicates that there is gene flow between the races. Craddock suggested that karyotypic differentiation at the racial level may be a normal stage in the speciation of many Phasmatodea.

Classification

It is now known that two species of *Phyllium*, not one, occur in the rain forests of north Queensland, apparently *P. siccifolium* L. (Fig. 19) and *P. frondosum* Redt. Both of these have previously been recorded from New Guinea; the second is possibly a

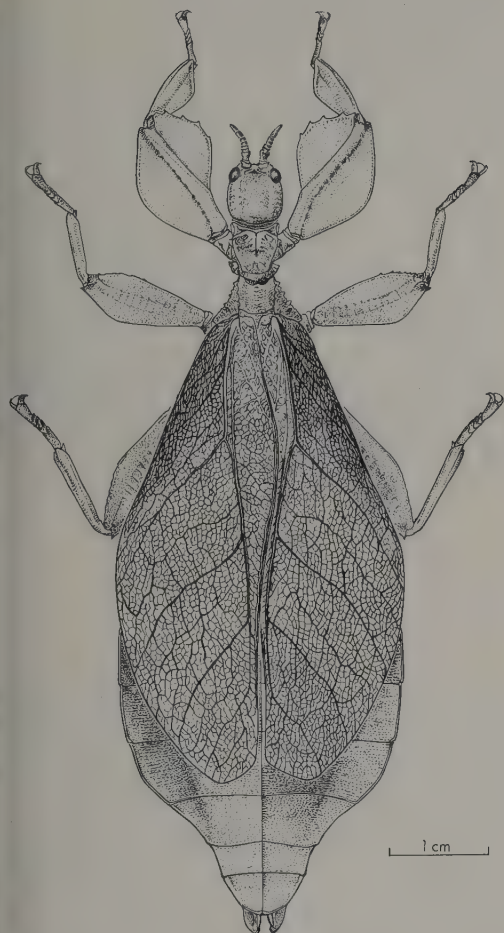


Fig. 19. *Phyllium siccifolium*, ♀. [S. Monteith]

synonym of the more widely distributed *P. pulchrifolium* Serv. Apart from this, it appears that the representation of the Phylliidae in Australia should be increased by the transfer to that family of the Necrosciinae, previously treated by modern authors as a subfamily of Phasmatidae. Although this subfamily lacks the triangular area at the ventro-distal extremity of the mid and hind tibiae that has been used as the principal diagnostic attribute of the Phylliidae, it possesses the sclerotized copulatory process of the tenth abdominal sternum known as the 'vomer'. None of the other Phasmatidae (only the Phibalosomatinae not checked) has a vomer, and the organ in the Necrosciinae is remarkably similar to its counterpart in *Phyllium*.* By this transfer the Australian Phylliidae come to comprise some 40 species and the Phasmatidae 90–100.

A further discovery is the occurrence on *Pandanus* in northern Queensland of *Megacrania batesii* Kirby, of which an earlier record from the Pellew Islands had been overlooked. This adds the Platycraninae to the subfamilies of Phasmatidae previously listed from Australia.

* Dr H. R. Roberts has now told me that two genera of Phibalosomatinae (a non-Australian group) and one of Lonchodinae, examined at my request, all have the vomer. Since none of the Australian genera referred to the Lonchodinae has a vomer, this subfamily may be composite. Application of the suggested new criterion would thus require transfer of the Phibalosomatinae, or at least some of its genera, in addition to the Necrosciinae, to the Phylliidae. Dr Roberts found that members of the Pygirrhynginae and Heteropteryginae, both placed in the Phylliidae, have the vomer, as expected.

EMBIOPTERA

(*Embiids, web-spinners, foot-spinners*)

by EDWARD S. ROSS

Ross (1970) has reviewed the biosystematics of the order and included appropriate references to the Australian fauna. The most primitive are found in tropical South America. This continent shares with Africa the distinction of having a much richer fauna than that of tropical Asia. The Asian fauna, which appears to have been the source of the three stocks found in Australia,

includes several elements totally distinct from those of South America and Africa. Inasmuch as the Embioptera appear to have evolved and dispersed in Gondwana, future analysis of the order may aid geologists investigating the fragmentation and drift of the continents. There have been no additions to the census of Australian species.

PSOCOPTERA

(*Psocids, booklice*)

by C. N. SMITHERS

Smithers (1967a) has published a catalogue of the Psocoptera of the world, which now comprise 2,200 species in 217 genera. Three genera and 11 species (5 Trogomorpha, 6 Psocomorpha) have been added to the Australian list (New, 1971a, b, 1972; Smithers, 1967b, 1971, 1972a, b). The viviparous species formerly included in *Archipsocus* have been transferred to *Archipsocopsis*.

In summarizing the economic significance of the order (p. 371), an observation by M. Watt (1965) that *Liposcelis bostrychophilus* Bad. could cause primary damage to stored products was overlooked.

An attempt has been made (Smithers, 1972c) to develop a phylogenetic classification of Psocoptera on the principles laid

down by Hennig (1966). It takes a strictly dichotomous form and differs considerably from the plan on p. 372, especially in the ranking of taxa. It has been put forward, at this stage, primarily for testing by workers familiar with the group.

The Permian-Jurassic Psocoptera (Permopsocida) are the sister-group of the two surviving suborders, which appear to have developed as separate entities in the second half of the Mesozoic, evolution of the families and genera probably occurring mainly in late Mesozoic and early Tertiary. A survey of their present distributions has revealed coherent patterns with a strong series of Ethiopian-Oriental elements, some of which extend into Australia. The 'Antarc-

tic' element is represented, as noted previously, particularly by the Sphaeropsocidae, and the link has been strengthened by removal of the South American and Australian species to a separate genus *Sphaeropsocopsis*. Comparison of native Australian and New Zealand Psocoptera (Smithers,

1970) showed, however, that the two faunas are not very closely related and certainly not wholly derived from a single ancestral fauna. Only a few groups, such as Philotarsidae and Elipsocidae, have much in common on opposite sides of the Tasman Sea.

25

PHTHIRAPTERA

(Lice)

by J. H. CALABY

Classification

Clay (1970) reviewed the characters and relationships of the amblyceran families, one biogeographically important finding being that the Trimenoponidae parasitizing South American marsupials and rodents are not closely related to the Boopidae of Australian-Papuan marsupials. In a critical examination of the order as a whole, she came to the conclusion that the Mallophaga are probably polyphyletic, and therefore proposed to drop the name and divide the Phthiraptera into four suborders—Amblycera, Ischnocera, Rhynchophthirina and Anoplura.

Australian Fauna

In the last few years, over 40 new species have been described from Australian hosts or from Papuan hosts that also occur in Australia, about half of them in miscellaneous papers on the large, bird-louse family **Menoponidae**, of which Clay (1969) provided an assessment of taxonomic characters and a key to the genera. In contrast, in **Laemobothriidae** the large number of nominal species of *Laemobothrion* (*Laemobothrion*), a subgenus restricted to the

Falconiformes, have been reduced to 4 valid species, of which 3 are cosmopolitan and have been recorded from Australian hosts (Nelson and Price, 1965). **Ricinidae** were known only from a Tasmanian thornbill (p. 383), but recent collections have established that species of *Ricinus* are parasitic on small passerine birds of several families in Tasmania and south-eastern Australia.

Kéler (1971) revised the **Boopidae** (7 genera, 35 spp.), including 14 new species from Australian-Papuan marsupials. The widely distributed *Heterodoxus spiniger* (End.) (p. 383) has been taken from a wallaby, and there is little doubt that its occurrence on dogs is a fairly recent secondary establishment. Clay (1971a, 1972) has corrected the spelling of the family name, and described 3 new species and a new genus, *Therodoxus*, from Papuan animals. *Therodoxus* is close to *Heterodoxus* and was founded on specimens from *Casuarius casuarius*, a large ground bird also found in Australia. It is apparently established on cassowaries, which extends the host range of boopids from marsupials to birds as well as canids. On the basis of new information,

Clay (1972) also reduced *Phacogalia*, a genus recognized by K  ler (1971), to synonymy in *Boopia*.

Among recently described **Philopteridae**, a distinctive new species of *Austrogoniodes* from Western Australia is apparently an established parasite of a diving duck,

Biziura lobata (Clay, 1971b), whereas the other 14 species of the genus are confined to penguins. Seven native species of *Hoplopleura* (**Hoplopleuridae**) have been described, all parasitic on native rodents (Kuhn and Ludwig, 1966; Kim, 1972).

26

HEMIPTERA

(Bugs, leafhoppers, etc.)

by T. E. WOODWARD, V. F. EASTOP and J. W. EVANS

Anatomy

The structure of the labrum and epipharynx of Heteroptera and its taxonomic and phylogenetic implications have been discussed by Stys (1969), and the innervation of the stylets of Homoptera and its probable function by Forbes and Raine (1973). Miles (1972) has reviewed the structure of the salivary glands and the composition and functions of saliva in the main groups of Hemiptera, and discussed their biological and evolutionary significance. Goel and Schaefer (1970) and Goel (1972) have endeavoured to establish a consistent terminology for the pretarsal structures. They consider that a true median arolium is probably absent in Heteroptera, and that the lateral pads at the bases of the claws should be termed 'pulvilli'. The median pair of processes, arising from a small apical extension (empodium) of the unguitactor plate, they term the 'parempodia', which are usually bristle-like. The presence or absence of the pulvilli, and their structure, are shown to be of taxonomic significance in the Heteroptera. The homologies of the ovipositor components of Pentatomoidea have been discussed by Schaefer (1968b).

Suborder HOMOPTERA

Schlee (1969) has suggested that the 'monophyly of Heteroptera and Coleorrhyncha is proved by the peculiarities of the antenna, wing, abdominal segments and cone and sclerite of the aedeagus' and that 'these synapomorphies evidence the Coleorrhyncha (Peloridiidae) as the closest relatives of the Heteroptera with whom they form a sister group'. He named the combined group Heteropteroidea.

PELORIDIOIDEA. In **Peloridiidae** Evans (1972a) erected a new genus *Hemio-woodwardia* for *Hemiodocus wilsoni* Evans and described *Hackeriella taylori* Evans from a relict population in north Queensland, which extends the northerly range of the family in Australia by some 560 km.

FULGOROIDEA. Fennah (1973a, b) has described a new species of **Delphacidae** from Lord Howe Island, providing evidence of relationship with New Caledonia, and a new cavernicolous species of **Meenoplidae** from Western Australia.

CERCOPOIDEA. The formation of the nymphal tube in **Machaerotidae** was dis-

cussed by Marshall and Cheung (1973). Evans (1970) described a new species of *Chaetophyes* from Queensland.

CICADELLOIDEA. The bionomics of leafhoppers have been reviewed by DeLong (1971). Evans (1968, 1969a, 1971, 1972b) has revised the tribal classification of **Cicadellidae**-Ulopinae; discussed the characteristics and components of the Ledrinae and Macropsinae; described 16 new Australian species; and discussed the characteristics and relationships of the Pentimiinae and Drabescinae and described new genera and species. Evans (1969b) described 4 new species of **Eurymelidae** from Australia. Strümpel (1972) proposed a system of classification in which 4 families—Membracidae, Aetalionidae, Bituritiidae and Nicomiidae—are brought together in a superfamily Membracoidea. The **Membracidae** are separated into 2 subfamilies, Membracinae confined to North and South America, and Centrotinae comprising the remainder.

PSYLLOIDEA. An account of the biology of psyllids with special reference to virus transmission has been given by Eastop (in Gibbs, 1973). None of the proven virus vectors has yet been identified from Australia. T. White (1973) has studied the aerial dispersal of *Cardiaspina densitexta* Taylor in South Australia. K. Moore (1970) gave an account of the genus *Glycaspis* (127 spp.), most of which feed on *Eucalyptus*.

APHIDOIDEA. C. Smith (1972) has published a comprehensive bibliography of work on aphids, and virus transmission has been reviewed by Watson and Plumb (1972) and Eastop (in Gibbs, 1973). Van Emden (1972) has given details of techniques for the study of aphids in the field and references to other sources of information about them. D. White and Carver (1971) have described adhesive vesicles, reminiscent of the circuli of Pseudococcidae, in some species of *Neophyllaphis*; Lindsay (1969) studied the cornicles (siphunculi, Fig. 26.16) of the pea aphid; Chen and Edwards (1972), discussing the structure and functions of cornicles, suggested that their sacs of lipid-secreting cells are

specialized accumulations of oenocytes; L. I. Gilbert (1967) summarized information on lipid metabolism and function; and Heie (1967, 1972) has described fossil aphids.

Buchner (1966) gave an account of microbial symbionts. Both sexes of Aphididae contain symbiotic organisms, whereas the males of Pemphigidae are symbiont-free. The Phylloxeridae are unusual in having no pseudovitelus and no other form of endosymbiosis.

Lowe (1973) contains reviews of several aspects of aphid biology, including polymorphism, biotypes, host-plant relationships and virus transmission. Pollard (1973) has given an extensive review of the penetration of plants by the mouth-parts; Pettersson (1973) has studied the olfactory reactions of *Brevicoryne brassicae* (L.) and given references to recent work on sex pheromones and host-plant selection; and Eastop (in van Emden, 1973, pp. 157–78) has analysed the distribution of host-plant specificity. Flight behaviour was reviewed by Kring (1972), and Marsh (1972) has recorded sex pheromones secreted by scent plaques on the hind tibiae of oviparae. Blackman (1972) investigated the inheritance of life-cycle differences in *Myzus persicae* (Sulzer) and gave references to recent work on the control of polymorphism.

Carver and White (1970) and Carver (1971) have described new and probably indigenous species from Australia.

ALEYRODOIDEA. Mound (in Gibbs, 1973) has given an account of the biology of **Aleyrodidae** with special reference to virus transmission; Butani (1970) listed publications on the family; and Mound and S. Halsey are preparing an annotated checklist, host-plant catalogue, parasite catalogue and bibliography.

COCCOIDEA. Morrison and Renk (1957) and Morrison and Morrison (1965) published bibliographies containing references to many earlier papers on Australian coccoids. Zimmerman's (1948) account of the Coccoidea of Hawaii includes species found also in Australia, and is probably the

most useful starting point for an Australian student. D. Williams (1973) has given an account of the coccoids found on *Macadamia* in Australia, and Brimblecombe (1968 and earlier papers) has recorded coccoids from crops in Queensland. Nur (1971) has reviewed the occurrence of parthenogenesis.

Howell and Kosztarab (1972) have revised the genus *Lecanodiaspis* (**Asterolecaniidae**) which contains many species living on native Australian trees, and D. Williams (1970, and in preparation) has given accounts of the **Pseudococcidae** of sugar-cane, rice and sorghum and the mealy bugs of Australia. In **Coccidae**, Snowball (1969, 1970) has provided information on economically important wax scales in Australia, and M. Williams and Kosztarab (1972) have illustrated and given notes on species that have been introduced to Australia. In **Diaspididae**, Brookes and Hudson (1968) described and keyed the nymphs and adults of the species of *Quadraspidiotus* on pome and stone fruits in Australia and summarized their distribution; McLaren (1971) and Willard (1972a, b) have written on the biologies of California Red Scale, *Aonidiella aurantii* (Mask.), and Yellow Scale, *A. citrina* (Coq.), on *Citrus* in Australia; Hudson (1967) listed the Tasmanian armoured scale insects and their host plants; and Takagi (1969–70) included species introduced into Australia in his account of the **Diaspididae** of Taiwan.

Suborder HETEROPTERA

DeCoursey (1971) has provided keys to nymphs of the North American families and subfamilies of Heteroptera. The nymphal scent glands of most groups open dorsally on the abdomen, and the number and position of the openings and associated areas are useful taxonomic features. In the pyrrhocorid *Dysdercus intermedius* Dist., Youdeowei and Calam (1969) obtained strong evidence that two of the glands produce an aggregating pheromone and a third a repugnatorial defensive secretion. Schaefer (1972a) concluded that the development of the adult metathoracic scent-gland apparatus in each of the major trichophoran groups of Heterop-

tera (those with abdominal trichobothria) is correlated with the habitat and biology of the bugs, there being, for example, usually higher development in ground-dwellers than in plant-dwellers of the same group and relatively poor development in aposematic bugs.

ENICOCEPHALOIDEA. Štys (1970a) discussed the higher classification of the Enicocephalinae and emphasized the unique position of the medial fracture between Sc and R on the fore wing of **Enicocephalidae**.

DIPSOCOROIDEA. The morphology and higher classification have been studied by Emsley (1969) and Štys (1970b); both emphasize the extremely isolated position of this group and propose to resurrect the taxon *Trichotelocera* Reuter to separate it from all other Heteroptera. Štys further divided it into 4 families—**Ceratocombidae**, **Dipsocoridae**, **Hysipterygidae**, and **Schizopteridae**. In the classification on pp. 400, 434, **Dipsocoridae** would become **Ceratocombidae**.

CIMICOIDEA. Couplets 4 and 5 in the key on p. 435 need to be replaced in order to accommodate the **Miridae**-**Isometopinae**, which are now known to occur in Australia.

4. Hemelytron without an embolium or cuneus; ♂ claspers symmetrical; more than 6 mm long **Nabidae**
Hemelytron with an embolium and (except in some brachypters) with a cuneus; ♂ claspers asymmetrical; lengths various 5
5. Membrane of hemelytron (except in some brachypters) with 1 or 2 closed cells near cuneus (Fig. 26.4b); labium obviously 4-segmented; ocelli absent, except in **Isometopinae** **Miridae**
Membrane of hemelytron with no basal cells; labium apparently 3-segmented; ocelli present **Anthocoridae**

Thaumastocoridae. The morphological studies of Cobben (1968) and Schaefer (1969) indicate an isolated position for this family, which Cobben placed in a separate superfamily **Thaumastocoroidea**. Slater (1973) discussed the feeding habits and the taxonomic and phylogenetic significance of nymphal and adult characters and described a new Australian species.

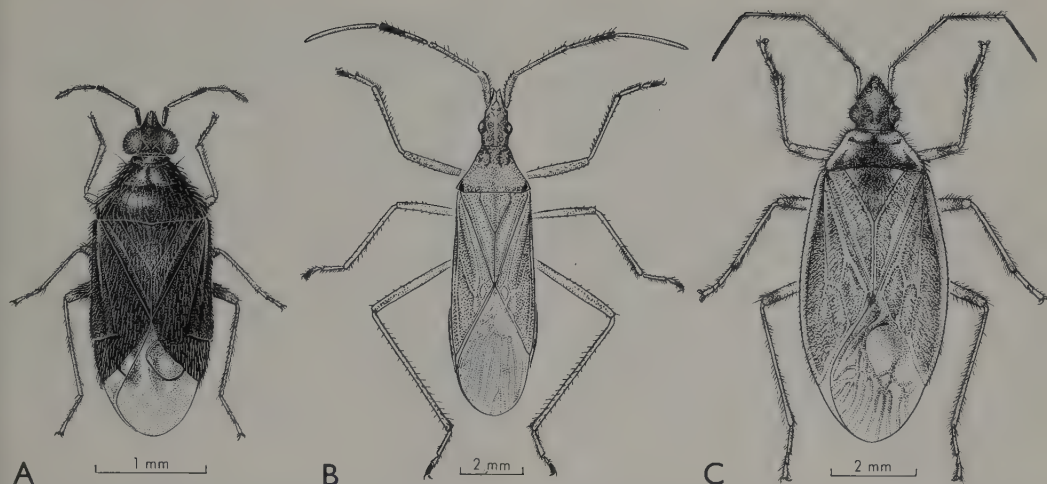


Fig. 20. A, Unidentified species of Miridae-Isometopinae; B, *Dicranocephalus* sp., Stenocephalidae; C, *Monteithocoris hirsutus*, Idiostolidae. [S. Monteith]

Miridae. The best-represented genus of the *Lygus* complex is *Taylorilygus*. Several *Drosera*-inhabiting mirids remain to be described from eastern and northern Australia. Eyles (1971-2) has briefly discussed the habitats and zoogeography of the Isometopinae and listed genera and species, including the one recorded Australian species (Fig. 20A). Slater and Schuh (1969) pointed out close similarities in the sclerotized areas of the female genitalia of isometopines with those of phylline mirids.

TINGOIDEA. Lee (1969) has discussed the taxonomic and phylogenetic significance of nymphal and adult characters in the **Tingidae**. The biological control of *Lantana* in Australia by *Teleonemia scrupulosa* Stål and other more recently introduced tingids has been reviewed by Harley and Kassulke (1971).

REDUVIOIDEA. The **Reduviidae**-Triatominae, which suck the blood of vertebrates, are now known by one species of *Triatoma* from northern Australia (Monteith, 1974). Louis and Kumar (1973) have discussed the comparative morphology of the alimentary and reproductive organs in relation to the higher classification of the family.

SALDOIDEA. On the basis of morphological studies of eggs, nymphs and adults, Cobben (1970) has erected a new saldoid family **Omaniidae**, distinguished most readily from Saldidae and Leptopodidae by small size (adults less than 2mm) and exclusively intertidal habitat, and a new genus *Corallocoris* to include all species in the Australian and Oriental regions previously placed in *Omania* (p. 441). Cobben (1968, 1970) uses the superfamily name Leptopodoidea.

ARADOIDEA. Pendergrast (1970) has removed the genus *Llaimacoris* from the **Aradidae**-Prosympiestinae, so that this subfamily is not represented in South America. The Chinamyersiinae (p. 442) are now known from the New Hebrides and New Caledonia, and Kormilev (1970, 1971b) also provided keys to the genera of Carventinae and Mezirinae of the Australian and adjacent areas.

COREOIDEA, LYGAEOIDEA. Recent work on the coreoid-lygaeoid complex still produces some conflicting opinions. Kumar (1968) has supported Štys in separating the Piesmididae as a superfamily; but his results do not give strong support for a close relationship between Largidae and Pyrrhocoridae, which have been brought together as

Pyrrhocoroidea by several authors and left in the Lygaeoidea by others.

Some modifications are required in the keys, mainly to make room for the Stenocephalidae and Idiostolidae which are defined below. In the key to superfamilies (p. 433), couplet 23, lines 2 and 5, delete 'brachypters with'; lines 3 and 6, for 'apex of head' read 'clypeo-labral suture'; line 4, for 'with no' read 'rarely with'. In the key to families of Coreoidea (p. 442), couplet 1, lines 4 and 8, for 'apex of head' read 'clypeo-labral suture'; line 7, for 'rarely with' read 'without' and insert 'usually' after 'antennifers'. In the key to families of Lygaeoidea (p. 444), couplet 1, line 5, for 'with no' read 'rarely with'.

Schaefer (1968a) extended his work on the morphology and higher classification of the **Coreidae**, and Allen (1969) revised the genus *Leptoglossus*. Chopra (1967) defined and keyed the subfamilies, tribes and genera of **Rhopalidae** and discussed their phylogeny. Štys (1964) discussed the morphology and relationships of **Hyocephalidae** within the coreoid-lygaeoid complex.

Stenocephalidae (Fig. 20B). Lansbury (1965-6) agreed with earlier workers that this family combines lygaeoid and coreoid characters. It would run to couplet 23 in the key to superfamilies on p. 433 and to couplet 2 in the key to families of Coreoidea on p. 443, but may be distinguished at both points by the following combination of characters: paraclypei acuminate and contiguous in front of clypeus; ovipositor lacinate; antennifers inserted below the line between centre of eyes and clypeo-labral suture. It is represented in Australia by two species of *Dicranocephalus*, the host plants known in other countries being Euphorbiaceae.

Lygaeidae. Woodward (1968a) established the subfamily Henicocorinae for *Henicocoris monteithi* Woodw. from south-eastern Australia; Hamid (1971) resurrected Stål's subfamily Cryptorhamphinae and redefined it; Malipatil (1973) described the nymph of *Cryptorhamphus orbus* Stål and compared it with the adult of this species and nymphs of other lygaeids; and Kehat and

Wyndham (1973) discussed the factors influencing flight activity in *Nysius vinitor* Bergr. Several lygaeid genera (e.g. *Noteolethaeus* and *Ethaltomarus*) are known only from Australia and southern Africa.

Idiostolidae (Fig. 20C). This small family, known only from South America and south-eastern Australia, exhibits a combination of plesiomorphic characters, particularly in the abdomen (Schaefer and Wilcox, 1969). It was formerly included in the Lygaeidae, from which it may be distinguished by having small submedian trichobothria on abdominal sternum 5 and 4 small lateral trichobothria on each side of sterna 6 and 7. The Australian genera *Trisecus* (2 spp.) and *Monteithocoris* (1 sp.) are 6-10 mm, subovoid, mirid-like bugs found on the forest floor near *Nothofagus* (Woodward, 1968b).

Piesmidiæ. Schaefer (1972b) considered that the Australian genus *Mcateella* and the Chilean *Miespa* had a common ancestor which, he suggested, may have entered Gondwana from the north.

PENTATOMOIDEA. Kumar (1969) proposed a tribal and subfamily classification of the **Tessaratomidae** based on studies of both adults and nymphs. McDonald (1969, 1970) described a second species of *Lestonia* and discussed the morphology of the **Lestoniidae** in comparison particularly with the related Plataspidæ. Kumar (1971) has studied the comparative morphology of the genitalia and alimentary system of **Urostyliidae**. In the **Pentatomidae**, Gross (1970, 1972) has revised *Cephaloplatus* (15 spp.) and synonymized *Eumecopus* with *Poecilometis*, which now includes 37 Australian species.

GERROIDEA. Møller Andersen (1969) provided a check-list of Australian *Microvelia* (**Veliidae**) and described a new species.

NOTONECTOIDEA. The key to families on p. 455 requires modification to accommodate atypical forms. In couplet 2 replace 'with femur thickened and . . . tarsus' by simply 'with femur greatly thickened', and replace couplet 3 by:

3. Connexiva of 4 abdominal segments clearly projecting lateral to margins of hemelytra; mid and hind tibiae with bristles, swimming hairs weakly developed or absent **Naucoridae**
- Connexiva of only 2 abdominal segments projecting lateral to margins of hemelytra; mid and hind tibiae with well developed fringes of long swimming hairs **Belostomatidae**

The genus *Anisops* (**Notonectidae**) has been revised by Lansbury (1969). In **Nepidae**, De Carlo (1968) described the male reproductive system of *Austronepe angusta* (Hale), and the genus *Ranatra* was revised by Lansbury (1972). La Rivers (1971) has described new tribes and genera of **Naucoridae** and compiled a world catalogue of taxa within

the family. *Aphelocheirus* is often placed in a separate family, Aphelocheiridae.

OCHTEROIDEA. Kormilev (1971a) has revised the Australian species of **Ochteridae**.

CORIXOIDEA. In **Corixidae**, Lansbury (1970) revised the genus *Sigara* and Wróblewski (1972) described a new species of *Micronecta*.

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27

THYSANOPTERA

(*Thrips*)

by L. A. MOUND

The Thysanoptera remain poorly known, despite much work in recent years. Most of this work in Australia has been taxonomic, but even this limited approach is far from complete. Very little is known about the biology of most species, although Lewis (1973) has reviewed the available information on the ecology of thrips, and Mound (in Gibbs, 1973) has given an account of their potential as virus vectors.

Anatomy

Mouth-parts. The feeding apparatus of thrips is usually thought to comprise two piercing maxillary stylets and a left mandible (p. 459). The mode of action of the stylets is

not clear and the mandible lacks a protractor muscle (Davies, 1969). However, recent studies with the scanning electron microscope have demonstrated that the maxillary stylets are mutually coapted to form a feeding tube in all groups of thrips (Fig. 21). The margins of each stylet are tongued and grooved, fitting together to enclose a median channel, but with no evidence of a salivary duct. The feeding aperture is subapical, and the apices of the stylets fit together with a complex of overlapping lobes (Mound, 1971c). The diameter of the median feeding channel varies between species, depending on the food ingested as well as the body size. In spore-feeding species the channel varies from

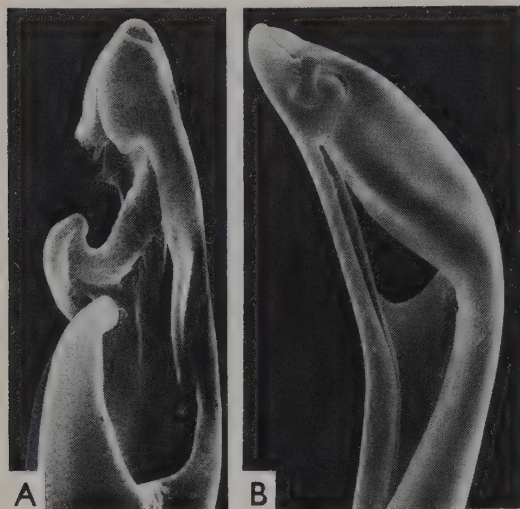


Fig. 21. A, *Idolothis spectrum*, Phlaeothripidae, apex of left maxillary stylet—the feeding aperture is the large opening in the lower foreground, $\times 1400$; B, *Diniothis sumatrensis*, Phlaeothripidae, apex of maxillary stylets of larva—right-hand stylet partly flexed with longitudinal tongue and groove detached, feeding aperture in central background, hook-shaped subapical lobe on left stylet corresponds to lobe at extreme left in A, $\times 900$. [Scanning electron micrographs by B. R. Pitkin]

4 to 8 μm in diameter, whereas it is only about 1 μm in most species that feed on green plants, although the stylets have essentially the same structure in all thrips. In many unrelated Tubulifera the maxillary stylets are elongate, extending into the head as far as the compound eyes, and in several species from *Casuarina* the stylets are convoluted, or even coiled (Fig. 22), apparently to facilitate penetration to the concealed chlorenchyma of these plants (Mound, 1970c). The mode of action of the maxillary stylets in thrips and the way in which food is ingested need further study.

The statement in Lewis (1973, p. 41) that the stylets of spore-feeding species are specially adapted for brushing and scraping spores towards the mouth opening was derived from a 1927 publication by A. Reyne. Comparison of Reyne's drawing with Fig. 21B suggests that this is a misinterpretation. The stylets are apparently protracted

alternately, and this involves the right-hand stylet flexing subapically. Reyne's figure merely shows a specimen with the right-hand stylet at maximum protraction and flexure relative to the left.

Legs. The functional morphology and homologies of the pretarsus in larvae and adults have been clarified by Heming (1971, 1972). The ungues, referred to as tarsal claws in most insects, project laterally in larval thrips, but are reduced to two spoon-shaped plates in the adults. They are rotated outwards by muscular contraction, and the protrusible bladder (the pretarsal arolium of other insects) lying between them is then dilated by blood pressure. The arolia apparently form an air-tight seal with the substrate. Most species jump before flying, but only a few have a highly modified thorax and hind legs (e.g. *Dendrothrips* spp.). *Kleothrips hardyi* Priesn. (Idolothripinae) has been observed to fly vertically upwards in a spiral (Mound, 1974), but the wing action of large thrips requires study.

Abdomen. The traditional terminology on p. 459 has to be modified as a result of Heming's (1970) study of the structure, development and homologies of the male and

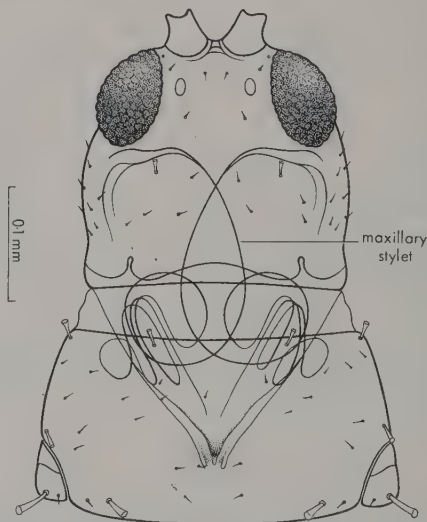


Fig. 22. *Adrothrips intermedius*, Phlaeothripidae, showing convoluted maxillary stylets.

[B. Rankin]

female terminalia. The male phallus is essentially similar in Terebrantia and Tubulifera. The phallobase bears a pair of parameres and is produced caudally into the phallosheath. Within this lies the invaginated but eversible endosheath bearing the more or less sclerotized aedeagus at its apex. The apex of the aedeagus sometimes varies between species (e.g. *Haplothrips* spp., Phlaeothripidae; *Odontothrips* spp., Thripidae, in Pitkin, 1972a), but the function of these interspecific differences during copulation and the method of transfer of the spermatophores require further study. Female Terebrantia usually have a well-developed ovipositor, in contrast to the Tubulifera, but the ovipositor is atrophied in a few Terebrantia (e.g. *Plesiothrips* spp., Thripidae; *Merothrips* spp., Merothripidae), although these species do not have the last abdominal segment elongate and tubular as in Tubulifera.

The Plague Thrips

Thrips imaginis Bagn., is generally regarded as a native species in Australia and New Caledonia. However, this is based on the negative evidence that *imaginis* has yet to be collected in any other country, and in view of the lack of collecting in Africa and Indonesia, this evidence is not very strong. More importantly, there are no close relatives of *imaginis* in Australia, as the other recorded species of *Thrips* are either Oriental or introduced from Europe. The native thrips found in the flowers of herbs and shrubs of Australia belong in the genera *Odontothripiella* and *Pseudanaphothrips* (Pitkin, 1972b). The genus *Thrips* is particularly well developed in Africa and Europe, and if *imaginis* is an immigrant, this might explain its remarkable host range on both native and introduced plants in Australia, as well as its freedom from predators and parasites.

Systematics and Biogeography

Rather more than 500 named species of thrips have been listed from Australia, although about 100 of these can be rejected as synonyms or *nomina nuda*. Of the remaining 400, only 140 are Terebrantia, but it is not

known if this represents an accurate proportion of the total fauna as this suborder is less well studied than the Tubulifera. In view of the number of species known from single specimens, it is likely that up to 1,000 species of Thysanoptera will eventually be found in Australia. Species recognition is complicated by allometric growth, the occurrence of morphs, and inter-population variation in non-vagile species (Mound, 1970a, 1972b). Two species of Merothripidae, probably introduced from America, have been collected recently from leaf litter in Australia (Mound and O'Neill, 1974). They may be distinguished from Aeolothripidae and Thripidae (p. 462) by their very small size, trapezoidal pronotum, and 8-segmented antennae with the segments more or less equal in length.

Many species of Thysanoptera are endemic to Australia, although there is a considerable number of introduced species (e.g. *Chirothrips* spp., in Mound and Palmer, 1972). Only in Queensland and the north of Australia are there many species with natural distributions outside Australia. Most of these are found in New Guinea or Indonesia, although a few are found in the Pacific. Three species from Queensland (*Gelothrips cinctus* Hood, *Habrothrips curiosus* Anan. and *Haplothrips pallescens* Hood) are known otherwise only from India, but may have a natural distribution in grasslands across the intervening area. The genera of Tubulifera feeding on green plants, such as *Acacia* (Mound, 1971a), *Casuarina* (Mound, 1970c) and *Geijera* (Mound, 1971b), are largely endemic, but those that feed on fungal spores or hyphae are frequently widespread, with representatives in Indonesia, New Guinea and the Pacific. This is to be expected in view of their biology and the readiness with which they are transported by wind (Mound, 1974). Only *Emprosthiotrips* (6 spp.) can be regarded as Bassian at present, but this is not surprising because thrips are basically a tropical group. Many genera of Terebrantia in Australia have a natural world-wide distribution (e.g. *Scirtothrips*, *Sericothrips*), and only a few of them appear to be endemic

(e.g. *Australothrips*, *Bhattithrips*—Mound, 1970b). Particularly interesting is the relatively large number of Aeolothripidae (24

spp. in Mound, 1972a), including two endemic species of *Dorythrips*, a genus known otherwise only from Chile and Argentina.

28

MEGALOPTERA

(Alderflies)

by E. F. RIEK

Mickoleit (Fig. 11) concluded that the female terminalia of Megaloptera are more advanced than those of Coleoptera. Larvae of *Austrosialis* are now known from silty, slow-

flowing sections of coastal streams; they are structurally similar to those of northern-hemisphere *Sialis* (Fig. 28.6 A). A revision of the Australian Megaloptera is in preparation.

29

NEUROPTERA

(Lacewings)

by E. F. RIEK

CONIOPTERYGOIDEA

Meinander (1972), in a monographic review of the **Coniopterygidae**, concluded that Coniopterygidae and Ithonidae represent primitive, independent sidelines from the main phylogenetic line of Neuroptera. The protruding labrum, straight, forwardly directed jaws, and reduced number of Malpighian tubes in the larvae of Coniopterygidae are primitive characters which are also found in Megaloptera. Australian

species were placed in *Heteroconis* (12 spp.), *Cryptosceneia* (4 spp.), *Spiloconis* (1 sp.), *Neosemidalis* (16 spp.) and *Coniopteryx* (8 spp.).

OSMYLOIDEA

This superfamily was based on a primitive attribute, the retention of nygmata in the wings; but it has proved to be composite and will require subdivision to reflect phylogeny. Riek (1974) revised the Australian **Ithonidae** (3 genera, 14 spp.), including a new genus

Megalithone which was inadvertently used prematurely in Fig. 29.2A and on p. 485. Zwick (1967) erected the **Neurorthidae** for the genera *Neurorthus* (Europe), *Nipponeurorthus* (Asia) and *Austroneurorthus* (Australia). The aquatic larva of *Neurorthus* is very similar to the presumed larva of *Austro-neurorthus* (Figs 29.11f, c).

MANTISPOIDEA

MacLeod and Adams (1968) studied the terminalia of **Berothidae**, particularly of the female. They confirmed the close relationship between Berothidae and Mantispidae, discussed evolution within the family, and defined 4 subfamilies. Most of the genera, and all recorded from Australia, were included in Berothinae. In the **Sisyridae**, Smithers (1973a) has described *Sisyra tropica* from north Queensland and given additional localities for species of *Sisyra*. The first-instar larvae of *Sisyra* usually inhabit the internal canals of the sponge where they are exposed to a moving stream of water, and they lack gills; whereas older larvae, living mostly on the surface, have articulated, segmented, ventral gills on the abdominal segments (Fig. 29.10c). All larval instars feed on sponge tissues, using one mandible-maxilla at a time as a probing and sucking mechanism.

HEMEROBIOIDEA

Tjeder (1966) and Adams (1967) both divided Recent **Chrysopidae** into 3 subfamilies—Apochrysopinae, Chrysopinae and Dictyochrysinae (=Nothochrysinae)—similarly delimited. They listed the genera of Dictyochrysinae, and Adams reduced the Mesozoic Mesochrysopidae to a fourth subfamily.

MYRMELEONTOIDEA

In a paper on Tertiary Neuroptera, MacLeod (1971) included the **Psychopsidae** with the myrmeleontoid families on the basis of larval morphology, described Ascalaphidae, Nymphidae and Psychopsidae from Baltic amber, and discussed the distinguishing characters of the larvae. Those of Recent **Nymphidae** have been characterized by the

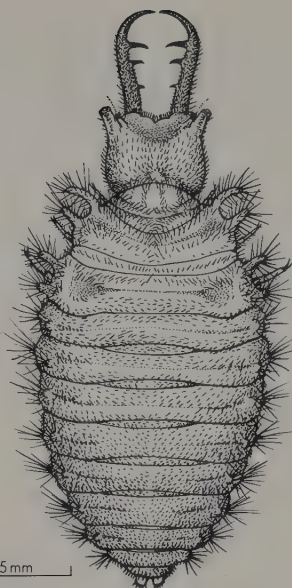


Fig. 23. Larva of *Aeropteryx linearis*, Stilbopterygidae. [S. Monteith]

presence of 1 mandibular tooth, compared with 3 or 4 in Ascalaphidae and Myrmeleontidae. In fact, though Ascalaphidae do have 3 teeth, Myrmeleontidae may have 1–4, and the fossil nymphid larva has 4 apparent teeth, of which 3 are rudimentary. Larvae of Nymphidae and Nemopteridae do not have tibia and tarsus fused in any leg and the stemmata are more or less sessile, whereas in other myrmeleontoids the tibia and tarsus are fused in the hind leg and the stemmata are usually grouped on a distinctly raised tubercle. The fossils show clear evidence of relationship with Recent genera in each of the families.

The larva of **Stilbopterygidae** (Fig. 23; McFarland, 1968) is similar to those of Ascalaphidae and Myrmeleontidae, but may be distinguished from them (couplet 13, p. 484) by the following combination of characters: lateral processes well developed on thorax, 2 on meso- and 2 on metathorax; abdominal segments with setigerous swellings; hind margin of head not markedly bilobed; hind tarsal claws enlarged. The larvae lie just below the surface of loose sand, with the mandibles spread at the surface. Riek (1968a) described the second stilbop-

terygid genus, *Aeropteryx* (2 spp.), and Kimmins (1970), describing the male of *A. linearis*, gave additional characters to distinguish *Aeropteryx* from *Stilbopteryx*.

Tjeder (1967) reviewed the **Nemopteridae** and stressed the differences between larvae of Crocinae and Nemopterinae. Crocine larvae are often long-necked as in Figure 29.12A, but some (e.g. Fig. 1965 in Tjeder) have comparatively short necks;

those of Australian *Croce* are still unknown. In contrast, nemopterine larvae are very similar to those of Myrmeleontidae, though the jaws lack teeth. A possible larva of *Chasmoptera hutti* recorded by Mathews (1947) appears to have been quite like the larval nemopterine illustrated by Mansell (1973, Fig. 1); both were found in loose surface sand. Koch (1967) revised *Chasmoptera* (3 spp.).

30

COLEOPTERA

(Beetles)

by E. B. BRITTON

A list of the families of Coleoptera of North America and the world, with estimated numbers of species, was published by Arnett (1967). The world total was estimated to be 290,119 (cf. 278,000 on p. 517) and the total for North America 28,600. As the total of Australian species already exceeds 19,000 and the fauna has been much less studied, it is likely that the number will eventually equal that of North America.

Anatomy

Recent important works on adult anatomy include a clear account of the skeletal structure of *Tenebrio molitor* by Doyen (1966), a study of the morphology and evolution of the prothorax in Coleoptera (Hlavac, 1973) and an exhaustive work on the morphology and function of wings and legs in Gyrinidae by Larsén (1966). Coaptation, briefly considered on p. 501, was the subject of an extensive study by Corset (1931). It is defined as the reciprocal fitting of two independent parts of the body which *together* have a definite function.

In contrast to the statement on p. 501, it is now known that, in some beetles at least, the elytra execute small movements in phase with the wings during flight and provide considerable lift. In *Oryctes boas* F. (Scarabaeidae-Dynastinae), a South African species, the elytra move through an angle of 20° as a result of the deformation of the thorax produced by the indirect flight muscles, and the mean angle of attack (the angle between the plane of the elytron and the direction of movement relative to the air) is 26°. At this angle the lift provided by the elytra was equal to 21 per cent of the body weight at the observed flight speed of 4 m.sec.⁻¹ (Burton and Sandeman, 1961).

Hinton (1967a) has described the structure and ecdysial process of the cribriform larval spiracles of the Scarabaeoidea. Gas exchange takes place through minute aeropyles, up to 4 μm long and 0.5 μm wide, in the C-shaped spiracular plate. The central bulla of the spiracle (Fig. 26B) is the scar marking the former external orifice of the ecdysial tube. In most preparations of these spiracles the

ecdysial tube is reopened by a splitting of the scar to form a curved slit. Because the aeropyles of the crescentic plate are so small and difficult to resolve, it has been commonly assumed that this adventitious slit was the true spiracular opening.

Social Parasitism

Coleoptera of many families have evolved an obligatory relationship with termites, ants, bees and wasps. Inquiline species are found in Carabidae, Histeridae, Staphylinidae, Pselaphidae, Ptiliidae, Scydmaenidae, Scarabaeidae, Limulodidae, Ptinidae, Clambidae, Dermestidae, Cucujidae, Silvanidae, Tenebrionidae, Cerylonidae-Aculagnathini, Colydiidae and Brenthididae. Little is known in most cases of the relationships between inquiline larvae or adults and their hosts, but it is clear that these cover the whole range from species which are purely predatory but specialize on a social insect as prey (e.g. larvae of *Sphallomorpha* spp.) through commensalism (tolerated scavengers) and parasitism to a relationship which amounts to symbiosis. Larvae and sometimes adults of the last group produce secretions which are eagerly sought by the host workers. The latter, in return, care for these highly specialized inquilines which are structurally adapted (e.g. by trichomes or physogastry) for the production of the secretions.

The larvae of *Sphallomorpha* (Carabidae; Fig. 27c) live in shallow vertical burrows on the periphery of the mounds of ants of the genus *Iridomyrmex* and prey upon passing ants in the manner of the larvae of *Cicindela*. They are equipped with dorsal hooks which anchor the larva in its hole and so prevent it being dragged out by the struggles of the prey (B. P. Moore, in preparation).

The Staphylinidae include a large number of termitophilous species, almost all of which belong to the Aleocharinae. The Australian fauna includes *Coptotermoecia*, *Hetairotermes*, *Nasutiphilus*, *Austrointhus*, *Termitoecia*, *Coptolimulus*, *Coptophilus*, *Drepanoxenus* and *Austrospirachtha* (Seevers, 1957; other refs on p. 39). The larvae of *Drepanoxenus* spp. are highly specialized

(Fig. 24) in body form, in the reduced suctorial mouth-parts, and in the presence of paired glands on each segment and a median gland on the eighth abdominal tergite. The adults also have four complexes of special glands. Workers of the host termite, *Drepanotermes* sp., are observed to groom the *Drepanoxenus* larvae especially in the vicinity of the glands, and when alarmed treat the larvae as they do their own. *Austrospirachtha mimetes* Watson (Fig. 25) is a remarkable aleocharine which lives in colonies of *Nasutitermes*. The abdomen of the adult becomes greatly inflated and recurved so as to cover the head and thorax and develops six 'appendages' and a bulbous posterior extension which give the insect a superficial resemblance to a termite worker. The subtribe Corotocina to which *Austrospirachtha* belongs is now known to be represented in South America, Africa, Madagascar and Australia, in association with the termite genera *Nasutitermes* and *Constrictotermes*.

Britton (1973) has recorded the species of *Pseudeba* (Tenebrionidae) that feed on the

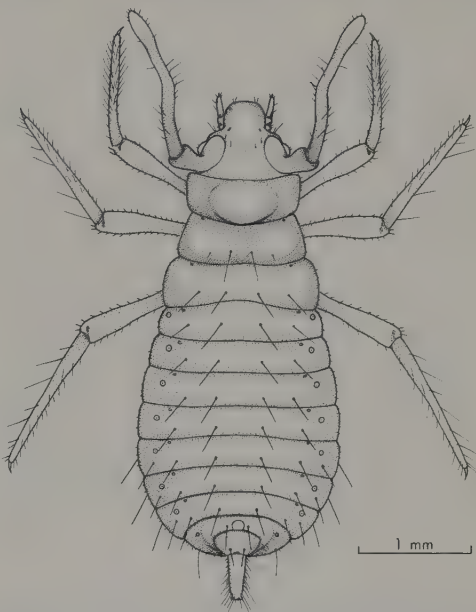


Fig. 24. *Drepanoxenus ardea*, Staphylinidae, larva, dorsal. [R. Kohout]

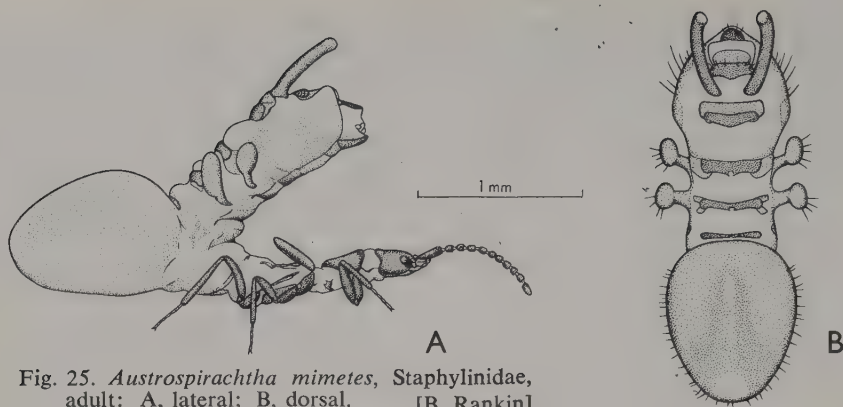


Fig. 25. *Austrospirachtha mimetes*, Staphylinidae, adult: A, lateral; B, dorsal. [B. Rankin]

dried grass and seeds stored in nests of *Drepanotermes* and *Nasutitermes*.

Defensive Mechanisms

In Coleoptera, defence against attack by bacteria and fungi as well as against predators is commonly achieved by means of chemical compounds secreted by special (usually pygidial) glands. Beetles may be protected, for example, by making their immediate environment strongly acid or basic. Silphidae are among the few beetles that produce an alkaline defensive substance, but the use of organic acids, such as formic and methacrylic, is frequent. Dytiscidae, which are particularly susceptible to infestation by aquatic micro-organisms, keep themselves clean by applying the secretion of their pygidial glands to the surface of their bodies at intervals while resting on a stem out of the water. The secretion contains phenolic compounds, especially benzoic acid and methyl p-hydroxy benzoate, which have a disinfectant action. On the other hand, they defend themselves against vertebrate predators, such as fish and amphibia, by secreting a milky fluid containing high concentrations of keto-steroids from reservoirs on the prothorax. This secretion stuns fish and is highly toxic to toads and mice (Schildknecht, 1970).

B. Moore and Wallbank (1968) have shown for Carabidae that, whereas the anatomy of the defensive mechanism is homologous throughout the family, the chemical compounds involved are surprisingly diverse.

Eight classes of compounds have been recognized: hydrocarbons; formic acid; higher saturated aliphatic acids; unsaturated aliphatic acids; saturated esters; simple phenols; salicylaldehyde; and quinones. The study of these secretions has taxonomic significance; for example, limitation of m-cresol to the secretions of the subfamilies Chlaeniinae and Panagaeinae supports a relatively close relationship deduced on other grounds. Although there is evidence of parallel evolution of chemical components, e.g. the widespread but scattered appearance of formic acid in the secretions, chemical composition is very uniform within genera and therefore useful as a means of recognizing phyletic lines at the generic level.

Larvae of Dermestidae-Anthreninae (including *Anthrenus*, *Anthrenocerus*, *Trogoderma*) possess a unique defensive mechanism in the form of entangling hairs. Serrate, spear-headed (hastate) setae are borne in dense tufts on the abdomen. When threatened by initial contact with a predator, such as an ant, the larva strikes with its posterior end, so that masses of hastate setae are detached and adhere to the appendages of the predator. The setae are not sticky, but because of their serrated shafts they become so entangled that the predator is unable to extricate itself and not infrequently dies (Nutting and Spangler, 1969).

Another specialized defence is exhibited by the larvae of Chrysomelidae-Cassidinae, which carry a mass of exuviae of earlier

instars mixed with faeces over their backs impaled on a long fork arising from the eighth abdominal segment (Fig. 28H). When disturbed by an insect predator, the larva swings the faecal mass to face the intruder, which is speedily discouraged (Eisner *et al.*, 1967). In contrast, when larvae of Chrysomelidae-Paropsini are irritated, they evert a pair of vesicles on the eighth abdominal tergite carrying drops of a defensive secretion which contains hydrogen cyanide, benzaldehyde and glucose and is lethal to ants (B. Moore, 1967).

The principal component in the surface-active secretion of the pygidial glands of *Stenus* (pp. 507, 546) has been identified as 1,8-cineole.

Immunotaxonomy

Serological studies of taxonomic relationships within Coleoptera have been made by Basford *et al.* (1968). Antisera were produced in rabbits by injecting saline emulsions of 24 species of beetles representing 15 families and tested serially against similar extracts made from 66 species of 24 families, using a quantitative precipitin test. The degree of relationship observed was very high between species belonging to the same genus, next highest between genera within the same family, and lowest between families, which indicates that the technique does measure relationships. Results in general supported current classification, although the indication of a close relationship between Carabidae and Gyrinidae was unexpected. A very high correspondence between Chrysomelidae and Cerambycidae suggested that these should be united in a single family, whereas Tenebrionidae were sharply distinguished from the other families tested.

Suborder MYXOPHAGA

The suborder was defined on p. 520, and further evidence for its validity is provided by the following characters of the larvae: presence of spiracular gills; arrangement of functional spiracles; and presence of a plastron. Spiracular gills and plastron respiration are found nowhere else among endopterygote

larvae. The area of the water-air interface over the spiracles is quite adequate to supply the oxygen requirements of these minute larvae, and they are able to breathe via the plastron when submerged or via the open spiracle when exposed to air, an arrangement well suited to the vicissitudes of life at the margins of streams (Hinton, 1967b). A criticism by Barlet (1972) of the validity of the suborder must therefore be discounted.

Suborder ADEPHAGA

Carabidae. The Australian Trechinae, including Tasmanian troglobites (p. 21), have been revised by B. Moore (1972). The subfamily now includes 10 genera and 43 species distributed among the tribes Trechodini, Perileptini and Trechini. Aepini have not been discovered, but it is possible that species of this tribe may yet be found in the intertidal zone on the southern coast of Tasmania. There is evidence that the Trechodini and part of the Trechini have descended from stocks which entered Australia, probably via Antarctica, before the Tertiary, whereas the Perileptini and the remainder of the Trechini (e.g. *Trechimorphus*, *Eutrechus*) are derived from later immigrants from the north. The genera *Agonica* and *Pseudagonica*, which run to Harpalinae in the key to carabid subfamilies (p. 525) are probably best treated as a separate subfamily Agonininae, distinguished from the Harpalinae by their strongly securiform labial palpi, pedunculate hind-body, and the absence of differentiated metepimera (in this resembling Carabidae-Simplicia). In a preliminary review of the Australian Paussinae, de Carvalho (1973) has defined *Megalopaussus (amplipennis* Lea) and seven species groups of *Arthropterus* and has provided a catalogue of species.

Dytiscidae. A key to the larvae of 18 genera of Dytiscidae has been provided by Watts (1963).

Suborder POLYPHAGA

There have been significant changes in the classification of the suborder. These are treated in more detail below, but may be

tabulated here to facilitate adjustment of the previous arrangement. Families added to the Australian list are indicated by an asterisk (*).

STAPHYLINOIDEA: Delete Scaphidiidae (p. 543), reduced to Staphylinidae-Scaphidiinae.

EUCINETOIDEA (new): Includes Clambidae (p. 557), Eucinetidae, Helodidae (p. 558).

DASCILLOIDEA: Now includes Dascillidae (p. 558), Rhipiceridae (p. 566), Karumiidae.

ARTEMOTOPOIDEA (new): Includes Artemotopidae, Callirhipidae (p. 566), Brachypsectridae.

RHIPICEROIDEA: Deleted.

DERMESTOIDEA: Add *Jacobsoniidae.

CLEROIDEA: Now includes Cleridae (p. 578), Chaetosomatidae, Phloeophilidae, Trogossitidae (p. 578), *Peltidae, Phycosecidae (p. 587), Melyridae (p. 571), *Lophocateridae, *Acanthocnemidae.

CUCUJOIDEA: Add *Protocucujidae, *Boganiidae, *Cavognathidae, *Phloeostichidae, *Lamingtoniidae, *Propalticidae, Prostomidae from Cucujidae-Prostominae, Dacoderidae from Tenebrionidae-Dacoderinae (p. 598). Delete Aculagnathidae (p. 594), reduced to Cerylonidae-Aculagnathini.

STAPHYLINOIDEA

Staphylinidae. Twenty Australian species of *Stenus* have been recognized in a recent review (Puthz, 1970). The genus is one of the largest known (ca 1,400 spp.) and is distributed throughout the world, with the exception of New Zealand. In addition to its unique method of propulsion on water the adult *Stenus* is remarkable for its elongate protrusible labium used for the capture of small prey such as Collembola. The labium can be forced out twice the length of the head and is drawn back by retractor muscles; its apex bears 3-segmented palpi and sticky setose paraglossae (Weinreich, 1968).

The larvae of the subfamilies of Staphylinidae have been described (with keys) by Kasule (1966), who has reduced the Scaphidiidae (p. 543) to subfamily rank in Staphylinidae on the grounds that their larvae differ from those of Staphylinidae less than the latter differ among themselves.

Anisotomidae. The Nemadinae with 9

genera and 31 species in Australia have been reviewed by Szymczakowski (1966).

SCARABAEOIDEA

Geotrupidae. The genus *Elephastomus* has been reviewed by Carne (1965).

Scarabaeidae. *Onthophagus* (Scarabaeinae) is the largest genus in the animal kingdom (world total over 1,500 species). The 165 Australian species have been reviewed by Matthews (1972), who has shown that prehensile claws, as seen in *Macropocopris*, have evolved more than once in the subfamily, so that *Macropocopris* should be treated as a synonym of *Onthophagus*. The fur-clinging habit of these species is an adaptation which enables the insects to exploit the faecal pellets of wallabies in spite of the hot dry climate of northern Australia (p. 123). More than 99 per cent of the microflora of the larval intestine in dung-feeding *Onthophagus* consists of bacteria, mostly anaerobic Clostridia which digest the cellulose that forms the food of the insect. This digestion occurs mainly in a large sac-like fermentation chamber which opens into the mid-gut (Halffter and Matthews, 1971). The introduction of exotic dung beetles to dispose of cattle dung in Australia is described on p. 24. Matthews (1974) has continued the treatment of Scarabaeidae with a review of the tribe Scarabaeini (16 genera, 94 species).

Larvae of *Sericesthis geminata* (Melolonthinae; p. 555) have been found to aggregate in areas of soil of high organic content and are able to develop in such soil in the absence of roots. They feed selectively on the organic matter and do not ingest the soil as a whole. The larvae also aggregate in soil containing roots, and roots are preferred to organic matter as food. Roots of grasses are preferred to those of *Trifolium repens* (white clover). It has been shown that the larvae are stimulated to feed by the sucrose, glucose and maltose (but not fructose) in the roots of forage plants (Wensler and Dudzinski, 1972).

The genus *Homalotropus* has been reviewed (Britton, 1970). There are 5 species in higher-rainfall areas of Queensland and northern New South Wales.

*Key to the Larvae of the Subfamilies of
Scarabaeidae*

1. Terminal segment of antenna reduced to an elongate cone at most half as wide as the penultimate segment (Fig. 32I), which has a defined hemisphere on the inner side at the apex 2
Terminal segment of antenna about as wide as the penultimate segment (Fig. 33E), which is without a sensory appendage on the inner side at the apex 3
2. Legs without claws or claws very small; body strongly humped (e.g. Fig. 30D); larvae in dung balls in soil SCARABAEINAE
Legs with well-developed claws; body of normal 'curl-grub' shape, not humped; larvae in dung or soil APHODIINAE
3. Anal cleft Y-shaped; terminal segment of abdomen usually with a well developed raster composed of a row or rows of stout spines on the ventral surface before the anus MELOLONTHINAE (part)
Anal cleft transverse; terminal segment of abdomen with or without a raster composed of longitudinal rows of spines 4
4. Raster with longitudinal rows of spines separated by a bare area
..... MELOLONTHINAE-Melolonthini
Raster not composed of distinct longitudinal rows of spines 5
5. Labrum symmetrical, with a deeply pigmented notch on each side of the middle of the distal margin; head partly covered by prothorax; abdomen with 9 segments visible dorsally; legs short, hind coxa shorter than width of clypeus (larva progresses on its back with legs uppermost) CETONIINAE
Labrum asymmetrical, with a deeply pigmented notch on the right side of the middle of the distal margin (Fig. 33E); head exerted; abdomen with 10 segments visible dorsally; legs long, hind coxa longer than width of clypeus 6
6. Stridulatory teeth on dorsal edge of maxilla always with anteriorly directed points (Fig. 30H); terminal segment of antenna with one dorsal and two ventral pale oval sensory areas; head never strongly punctured or dark brown RUTELINAE
Stridulatory teeth on dorsal edge of maxilla bluntly rounded (Fig. 30G); terminal segment of the antenna usually with more than 3 pale oval sensory areas; head usually strongly punctured, sometimes very dark brown DYNASTINAE

EUCINETOIDEA

Established by Crowson (1967) to include the Clambidae, Eucinetidae and Helodidae from the Dascilloidea. The adults have a transverse metasternal suture which does not extend to the lateral margins, wings with 4 anal veins, and hind coxae with the posterior face vertical and more strongly excavate than in Dascilloidea. The larval spiracles are annular and have a closing mechanism.

DASCILLOIDEA

Having established the Eucinetoidae, Crowson (1971) united the remaining family Dascillidae with the Rhipiceridae from Rhipiceroidae and Karumiidae from Cantharoidea in a revised Dascilloidea with the following characters. Adults with prosternal process not received into a cavity on the mesosternum; fore coxae conical, projecting, the cavities open behind; prothoracic hypomera with a knob or process on each side which is received into a corresponding cavity of the mesothorax; metasternum with a complete transverse suture; hind coxae with a steep posterior face against which the hind femur can be received; abdomen with 5 free sternites; tarsi 5-5-5-segmented; abdomen with functional spiracles on segment 8; aedeagus trilobate, the median lobe divided into dorsal and ventral sclerites; metendosternite without sclerotized arms; antennae filiform, serrate or pectinate, without a terminal club; Malpighian tubes with free ends. Larvae without urogomphi, with well developed galea and lacinia and a mandibular mola.

Adults of the two families known in Australia may be distinguished by the following couplet.

With a plurisetose empodium between the claws; antennae inserted on prominences on top of head; tibiae with small teeth along outer edges; hind margin of pronotum finely crenulate **Rhipiceridae**

Without an empodium between the claws; antennae not inserted on prominences; tibiae without small teeth; hind margin of pronotum not crenulate **Dascillidae**

DRYOPOIDEA

Helminthidae: Hinton (1968) has provided a key to the 11 (9 Australian) subgenera of *Austrolimnius*. **Heteroceridae:** The Australian species have been reviewed (Charpentier, 1968). Two of the 3 known genera and 8 species are found in Australia. The 7 species of *Heterocerus* are very close and appear to be the product of recent evolution. **Limnichidae:** A new subfamily Hyphalinae has been erected for *Hyphalus insularis* Britton, found in the intertidal zone on the Great Barrier Reef and the coast of Queensland (Britton, 1971). **Psephenidae:** The morphology and biology of the larvae and pupae of *Sclerocyphon* (6 spp.) were described by Bertrand and Watts (1965).

RHIPICEROIDEA

This superfamily has been suppressed, the Rhipiceridae having been removed to Dascilloidea and the Callirhipidae to Artemotoipoidea.

ARTEMOTOPOIDEA

A superfamily of Elateriformia established by Crowson (1973b) for the families Artemotopidae (=Euryopgonidae) from Dryopodea, Callirhipidae from Rhipiceroidea and Brachypsectridae from Cantharoidea. Only Callirhipidae are known to occur in Australia. Adults with excavate or sharply declivous hind coxae (as in Elateridae); antennae without a club (but strongly flabellate in Callirhipidae); fore coxal cavities fully open behind; abdomen with only 5 sternites and a sharp intercoxal keel (unlike Cantharoidea); functional spiracles on segment 8, and a simple trilobate aedeagus with an undivided median lobe; metasternum without a transverse suture (unlike Buprestoidea); abdominal tergites 1–6 membranous (unlike Buprestoidea); hind angles of the prothorax not acute and without thoracic 'clicking' mechanism (in contrast to Elateroidea), but with a prosternal process received into a mesosternal cavity. The larvae have fully developed thoracic legs; head with a distinct articulated labrum, without a fronto-

clypeal suture; mandibles without a mola; maxillae with articulating area reduced or absent, the galea blunt and articulated; spiracles biforous; one stemma on each side; 2 setae on each claw. In the key to superfamilies of Polyphaga (p. 534) the superfamily runs to Rhipiceroidea which it replaces.

CANTHAROIDEA

Lampyridae. In a review of the tribe Luciolini, Ballantyne (1968) has reduced the Australian *Atyphella* to subgeneric rank in *Luciola*. The distribution of Lampyridae is now known to include north and western Australia, and a second genus, *Pteroptyx*, is represented in north Queensland by *P. cribellata* (Oliv.) which is widely distributed in New Guinea and New Britain (Ballantyne and McLean, 1970). Whereas the function of the luminous organs of adult Lampyridae in bringing the sexes together is well established, that of the well-developed luminous organs of the larvae of some species has been obscure. Kaufmann (1965) suggested that ovipositing females avoid larval lights on the ground, and are thus induced to migrate to less crowded areas.

DERMESTOIDEA

Dermestidae. A world catalogue has been published by Mroczkowski (1968), including 89 Australian species, of which 46 belong to *Trogoderma* and 21 to *Anthrenocerus*. Stridulation by adult *Dermestes lardarius* has been recorded by Bailey (1967).

Jacobsoniidae (= Sarothriidae). Represented in the Australian fauna by undescribed species (E. Hamilton-Smith, personal communication). Small (2 mm) beetles with a greatly elongate metasternum, which is longer than all other ventral segments; antennae filiform or clubbed; mouth-parts reduced and hidden by the mentum; hind coxae widely separated; tarsi reduced, 2- to 5-segmented. Found under bark, in leaf litter, or in bat guano.

BOSTRYCHOIDEA

Ptinidae. Lawrence and Reichardt (1969) have reviewed the myrmecophilous Ptinidae

and given a key to the Australian genera (*Diplocotes*, *Enasiba*, *Ectrephes* and *Polyplocotes*, total 35 species).

CLEROIDEA

The superfamily now includes the Cleridae, Chaetosomatidae, Phloeophilidae, Peltidae, Trogossitidae, Phycosecidae, Melyridae, Lophocateridae and Acanthocnemidae (keys in Crowson, 1970).

Peltidae. Formed by a division of Trogossitidae and now (Crowson, 1970) includes 4 subfamilies—Decamerinae (American), Peltinae (Holarctic), Protopeltinae (New Zealand) and Rentoniinae (Australia, New Zealand, Chile). The only Australian species is *Parentonium australicum* Crowson from the mountains of south Queensland.

Lophocateridae. Erected by Crowson (1970) for the Trogossitidae-Lophocaterinae. It is distinguished from Trogossitidae by the open fore coxal cavities and well developed lacinia. The only representative is *Floricator pusillus* Crowson from the coast of New South Wales.

Acanthocnemidae. Based by Crowson (1970) on *Acanthocnemus nigricans* Hope, a species of southern Queensland origin which has been introduced into the Mediterranean region, Madagascar and New Caledonia. It was thought to be a primitive melyrid, but is distinguished from that family by the presence of an antennal club, simple claws, spines on the outer edges of the tibiae, and large pits on the hypomera of the prothorax.

Trogossitidae. The Tasmanian *Egolia variegata* Erich. and *Necrobiopsis tasmanicus* Crowson have been restored from Peltidae to the Trogossitidae-Egoliinae by Crowson (1970).

Phycosecidae. Transferred from Cucujoidea to Cleroidea by Crowson (1967), the single genus *Phycosecis* runs to 'Cucujoidea, pt.' in couplet 38 of the key to the superfamilies (p. 536). It can be distinguished from other Cleroidea by its dense clothing of white scales and the absence of erect setae.

Melyridae. The larvae of Melyridae resemble those of the cleroid families much

more closely than those of Cantharidae. The similarities include the presence (except in Peltidae) of a curious pedunculate seta on the lacinia. The similarities of adult Melyridae and Cantharidae are ascribed to degenerative convergence, the result of a short free-living adult life associated with a chemical defence.

CUCUJOIDEA

Protocucujidae. The family was erected by Crowson in 1955 for his Chilean genus *Protocucujus*, later synonymized with *Ericmodes* by Crowson (1967).^{*} This is probably the most primitive of the cucujoid families, showing affinities to the Cleroidea (Trogossitidae), Chrysomeloidea, Curculionoidea (Belidae) and Heteromera. *Ericmodes* now includes two Chilean species and *E. australis* Grouv. from Australia which was formerly placed in the Nitidulidae. In the key to the families of Cucujoidea (p. 581) *Protocucujidae* run to couplet 8 'Cleroidea-Trogossitidae, pt.' from which they may be distinguished by the absence of numerous erect setae or scales.

Boganiidae. A family erected by Sen Gupta and Crowson (1966, 1969a) to include the genera *Paracucujus*, *Hydnobioides*, *Boganium* and *Hobartius*. Small beetles, length 2–4 mm, resembling Cryptophagidae; antennae with 3-segmented club; frontoclypeal suture present; mandible with a dorsal tubercle on its basal half, often with a seta-fringed cavity (mycangium) on the inner side of the tubercle; maxillae with distinct galea and lacinia, palpi with apical segment narrow, elongate; pronotum without lateral longitudinal carinae or basal impressions; fore coxal cavities open, trochantin visible; mesepimera reaching the mid coxal cavities; elytra reaching the apex, but outer edge distinct only in basal third; tarsi 5-5-5-segmented, claws simple; hind wings usually present. The family runs to couplet 10 in the key to Cucujoidea (p. 581) and is distinguished from Cryptophagidae and Silvanidae

^{*} Under Article 40 of the *International Code of Zoological Nomenclature*, 1961, this action does not affect the name of the family.

by the dorsal mandibular tubercle and mycangium. A key to the related families is given by Crowson (1973a).

Mandibular mycangia, present in *Paracucujus* and *Boganium*, are found also in Sphindidae, Cavognathidae, some Phloeostichidae and some Cucujidae. These cavities probably serve for the transport of spores necessary for the digestion of some unusual food.

Cavognathidae. Erected by Sen Gupta and Crowson (1969a, 1973) to accommodate *Cavognatha* (Australia), *Zeonidicola*, *Neocercus* (New Zealand) and *Taphropiestes* (Chile). Small beetles, very like Cryptophagidae-Cryptophaginae; antennae with 3-segmented club; head with a slight constriction behind the eyes; fronto-clypeal suture absent; mandible with one or two mycangia opening outwardly; maxilla with galea and lacinia, the palp not securiform; prothorax without lateral carinae or impressions; fore coxal cavities open, trochantin partly exposed; epipleura extending to the apices of the elytra but clearly defined by a ridge only towards base and apex; mesepimera reaching the mid coxal cavities; tarsi 5-5-5-segmented; hind wings present; sutural edges of the elytra separated in the apical sixth. The family runs to couplet 10 in the key to Cucujoidea (p. 581) and is distinguished by the gape of the elytra near the apex. A key to the related families is given by Crowson (1973a).

The only Australian species is *Cavognatha pullivora* Crowson, of which the adults are found only in nests and the larvae on nestlings of the Australian magpie (*Gymnorhina tibicen*).

Phloeostichidae. Proposed by Sen Gupta and Crowson (1969a) for 4 genera from Europe, Chile and New Zealand and 6 species from Australia, *Priastichus tasmanicus* Crowson, *Hymaea* (4 spp.) and *Anaplopus tuberculatus* Blkb. which had been placed by Abdullah in Tenebrionidae-Anaplopinae. Length less than 10 mm; head sometimes with a constriction behind the eyes, without a fronto-clypeal suture; antennae with a weak 3-segmented club; mycangia, if present,

opening on dorsal surface of mandible; prothorax with fore coxal cavities partly closed; mesepimera reaching the mid coxal cavities; elytra, except in apterous forms (*Priastichus*), with a distinct sutural gape in the apical quarter; tarsi 5-5-5-segmented in ♀, 5-5-4 in ♂. A key to the related families is given by Crowson (1973a).

Lamingtoniidae. Erected by Sen Gupta and Crowson (1969b) for *Lamingtonium binnaburrense* Crowson. Small beetles (ca 3.5 mm) distinguished by: tarsi 5-5-5-segmented, 1st segment as long as 2nd; mesepimera reaching the mid coxal cavities; the fore trochantins partly exposed; fore coxal cavities open behind; spiracles present on abdominal segments 1-7; fore tibia without longitudinal keel or denticles; antennae with 3-segmented club; elytra entire, not truncate; head not constricted behind the eyes; mandibles without cavities or dorsal tubercles; fronto-clypeal suture absent; elytral epipleura complete; gular area broad. The family runs to Languriidae in the key to cucujoid families (p. 581), and is distinguished by the mesepimera reaching the mid coxal cavities and exposure of the fore trochantins.

Propalticidae. Represented in Australia by *Propalticus doddi* John and *P. simplex* Crowson and Sen Gupta (1969), which are found under the bark of dead trees and probably feed on fungal spores. Very small beetles (less than 2 mm); antennae 10- or 11-segmented, scape and pedicel markedly larger than other segments, club narrow, elongate, 3-segmented; mandible with large mola, 3 apical teeth and molar asperities extending on to the dorsal surface; maxilla with broad setose galea and glabrous lacinia with 2 apical hooks; apical segments of palpi cylindrical; prothorax large, narrowed anteriorly, with strongly curved sides and a median longitudinal groove, but without basal impressions; all coxae widely separated; fore coxal cavities open behind; elytra short and broad with longitudinal carinae, usually setose or squamose; elytral epipleura extending to apices; scutellum large and strongly transverse; mesosternum short, the coxal cavities closed by the meso- and metasterna;

metasternum with median line complete; tarsi 5-5-5-segmented, segments 1 to 4 simple and about equal in length; fore tibia with a large, spatulate, serrated spur; abdomen with all segments free.

Propalticus runs to Cryptophagidae in the key to cucujoid families (p. 581), but is distinguishable by the very large prothorax with median groove, the large, spatulate, serrate spur on the fore tibia, and the slender antennae with large scape and pedicel. The family is most closely associated with Languriidae and Cryptophagidae. It is probable that all species of *Propalticus* will be found to jump, using the fore legs activated by powerful muscles in the large prothorax.

Cerylonidae. Besuchet (1972) and Sen Gupta and Crowson (1973) have shown that *Aculagnathus* should be included in the Ceryloninae, so that Aculagnathidae falls into synonymy.

Prostomidae. Erected by Crowson (1967) to include Cucujidae-Prostominae (Australian genus *Prostomis*), to which it runs in the key to families (p. 582). World species 22, Australian 4.

Tenebrionidae. J. Watt (1967a) has reviewed and compared earlier subfamily classifications. Alleculidae (p. 599) are clearly a specialized branch of the tenebrionid stock and can be preserved as a family only if Tenebrionidae is broken up. Watt (1967b) has erected 2 new families, Perimylopidae to include 4 genera from South Georgia, the Falkland Islands and Tierra del Fuego, and Dacoderidae based on the Dacoderinae (p. 598).

Dacoderidae. Beetles of narrow, convex form, ca 11 mm long; antennae short, stout, 10-segmented, without a club; head rostrate; mouth-parts concealed by a large mentum; labrum covered by clypeus; terminal segments of palpi fusiform; galea and lacinia setose; prothorax cylindrical with very deep transverse and longitudinal depressions; fore coxal cavities almost closed behind; mid coxal cavities closed by the sterna; elytra non-striate; hind wings present; tarsi 5-5-4-segmented, segments not lobed; claws and tibial spurs simple; abdominal sternites free.

Dacoderidae are most closely related to Salpingidae, to which they run in the key on p. 584, but may be distinguished by their large mentum, non-striate elytra, weakly transverse hind coxae, and deep furrows on the prothorax.

Othniidae (=Elacatidae). Although *Elacatis* has priority over *Othnius*, the family name Othniidae has priority over Elacatidae. One species, *Elacatis delusa* Pascoe originally found in Borneo, was discovered in north Queensland (p. 518n.). It is 5 mm long; prognathous; antennae slender, with a well marked 3-segmented club; terminal segments of palpi parallel-sided and truncate; mentum scarcely emarginate; lateral edges of pronotum scalloped (undulating in outline); fore coxae oblique, rounded, projecting, the cavities fused and almost closed behind; mid coxal cavities closed by the sterna; hind coxae strongly transverse with a transverse groove; abdominal sternites apparently free; tarsi very slender, 5-5-4-segmented, the proximal and distal segments elongate; entire surface (except gula) pubescent; elytra with a dark brown pattern on a yellowish ground. In the key to cucujoid families (p. 584) this species runs to Salpingidae, which differ in having open fore coxal cavities and in lacking defined lateral prothoracic edges.

Coccinellidae. Sasaji (1968) has proposed a new classification based on both larval and adult characters. Six subfamilies and 18 tribes are defined, with keys. The biology of the family has been reviewed by Hodek (1973). The large subfamily Epilachninae is represented in Australia by 7 species of *Epilachna*, only 3 of which are endemic (Bielawski, 1963). The 3 Australian species of *Stethorus*, predators on the two-spotted mite *Tetranychus urticae*, have been reviewed by Britton and Lee (1972).

CHRYSOMELOIDEA

Cerambycidae. The Australian genus *Strongylurus* (14 spp.) has been reviewed by Elliott and McDonald (1972).

Chrysomelidae. *Microdonacia* was originally placed in the Donaciinae by Blackburn, but was transferred to Eumolpinae by

Monrós. Jolivet (1968) has now proved that the genus belongs to the Halticinae. *Donacia australasiae* Blkb. remains the only species of the aquatic Donaciinae recorded (and as yet unconfirmed) in Australia.

Key to the Larvae of the Subfamilies of Chrysomelidae

1. Labrum not clearly visible; legs long and slender; body C-or J-shaped, the caudal segments swollen; larva sometimes enclosed in a dark case (Fig. 31I, J) CLYTRINAE, CRYPTOCEPHALINAE
Labrum clearly visible; larva not in a case 2
2. Mandible with 1-3 distal teeth; stemmata (p. 1) absent; maxillary palpi 4-segmented; in soil, feeding on roots EUMOLPINAE
Mandible with a row of 3-5 more or less equal distal teeth (e.g. Fig. 32J, K); stemmata usually present; maxillary palpi 2- or 4-segmented; feeding on leaves 3
3. Abdominal segment 8 bearing 2 long, upright, sclerotized processes on which a mass of exuviae and faeces is borne; segments of thorax and segments 1-7 of abdomen with long, laterally directed spiny processes (Fig. 28H) CASSIDINAE
Abdominal segment 8 without a pair of upright processes; segments of thorax and abdomen without long, spiny processes 4
4. Maxillary palpi 2-segmented; abdomen 8-segmented (e.g. Fig. 27A); legs 3-segmented, or absent; each claw with a bifurcate pulvillus beneath; includes some leaf-miners HISPINAE

- Maxillary palpi 3- or 4-segmented; abdomen 9- or 10-segmented; legs 4-segmented 5
5. Head with 5 or 6 stemmata on each side ... 6
Head without stemmata, or with 1 stemma on each side 7
 6. Labial palpi 1-segmented; with 2 rows of 'pseudopod' swellings on ventral side of the abdomen (Fig. 31F); anus opening upward or posteriorly; body covered with faeces CRIOCERINAE
Labial palpi 2-segmented; abdomen without 'pseudopod' swellings; anus opening downward in the middle of a sucker-disc on segment 10 (Fig. 31E) CHRYSOMELINAE
 7. With a single stemma on each side of the head GALERUCINAE
Without stemmata HALTICINAE

CURCULIONOIDEA

Curculionidae. The genus *Catasarcus* (Leptopiinae; 42 spp.) has been reviewed by R. Thompson (1968). It is limited to Western (mainly south-west), central and South Australia. Uther Baker (1972) has defined and reviewed the genus *Notonophes* (Amycterinae). The Australian fern weevils of the subfamily Phrynixinae have been reviewed by Kuschel (1972). One species, *Syagrius intrudens*, introduced from Australia into Ireland and Hawaii has not yet been found in its homeland, where the genus is precinctive.

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KEY TO FAMILIES OF COLEOPTERA BASED ON LARVAE

by E. B. BRITTON

The following key to the more important families of beetles has been prepared from available Australian larvae and from characters abstracted from works on larvae by Böving and Craighead (1931), Chu (1949), Peterson (1960) and Usinger (1956). The families included cover 98 per cent of Australian species. An effort has been made to make the key as practical as possible, but it should be used with caution because it is based on a very limited number of species.

Before entering the key, it is necessary to

be sure that the larva is that of a beetle, and it should therefore be checked against the following combination of characters (see also pp. 508-9).

With a well-developed, fully sclerotized head, without compound eyes; mouth-parts adapted for chewing; maxillary palpi present; labium without a median conical spinneret; antennae with 2 or more segments, inserted within the anterior arms of the Y- or V-shaped ecdysial lines; ventral abdominal prolegs, if present, on at most 3 segments,

and without crochets; if without prothoracic legs, the head is almost always hypognathous and the body crescent-shaped or thicker in the middle; if with long, filamentous abdominal gills, the abdomen is terminated by a conical process with apical hooks and the labrum is absent.

In the key, the term *mola* applies to a grinding surface at the base of the inner face of a mandible, whereas *mala* refers to the lobe of a maxilla when only one lobe is present. When two lobes are present, they are referred to as the *galea* (outer) and *lacinia* (inner).

1. Terrestrial larvae 2
Larvae living in water, in wet mud, sand, or gravel, or in the intertidal zone 105
- 2(1). With paired processes (2 or 4, segmented, unsegmented or hook-like) on the 8th or 9th abdominal segment (e.g. Figs 27H, 28A, 31H), the processes sometimes covered by a dark mass of exuviae and faeces (Fig. 28H) 3
Without paired processes on the 8th or 9th abdominal segment 41
- 3(2). Legs 5-segmented (coxa, trochanter, femur, tibia, tarsus) and one or two claws; labrum absent (Figs 28C, F) **Carabidae**
Legs 4-segmented (coxa, trochanter, femur, tibiotarsus) and one claw; labrum present or absent 4
- 4(3). Abdomen 8-segmented; mouth-parts often directed forwards and upwards
..... **Hydrophilidae**
Abdomen 9-segmented; mouth-parts directed forwards or forwards and downwards 5
- 5(4). Apical abdominal processes in the form of long setae; body small (<5 mm), tapered to one or both ends (often found clinging to the appendages of bees or flies) 6
Apical abdominal processes segmented or articulated on the 9th abdominal segment (i.e. with a discontinuity in the form of a pale line between process and tergite) (e.g. Fig. 28A) or with 2 long, unsegmented processes arising from the 8th tergite and bearing a faecal mass (Figs 28H, 31H) 8
Apical abdominal processes short, often hook-like, fused to the 9th abdominal tergite (e.g. Fig. 27H) 11
- 6(5). Mandibles distinct; antennae obvious, 2- or 3-segmented; head with at most a single stemma (p. 1) on each side 7
Mandibles and antennae absent; eyes large, composed of 3-5 stemmata; claws setiform, single (Fig. 31.5) 1st instar larva ('triungulinid') of Strepsiptera
- 7(6). Claws with a stout seta on each side, giving a 3-clawed appearance (Fig. 26A)
..... 1st instar larva ('triungulin') of **Meloidae**
Claws single, with a slender seta on each side 1st instar larva of **Rhipiphoridae**
- 8(5). All segments bearing long, spiny processes laterally (and anteriorly on the pronotum); exuviae of earlier instars and faeces borne in a mass on two long erect processes which arise from the 8th tergite (Fig. 28H) **Chrysomelidae-Cassidinae**
Body without spiny processes on all segments 9
- 9(8). Body of flattened 'trilobite' form (Fig. 28E); paired processes on 9th abdominal segment short and thick (associated with carrion) **Silphidae**
Body subcylindrical, the segments without flattened lateral extensions; paired processes on 9th abdominal segment often long and slender (e.g. Fig. 28A) 10
- 10(9). Antennae and palpi long; antennae 4-segmented; spiracles simple, with a single opening
..... **Staphylinidae**
Antennae and palpi short; antennae 3-segmented; spiracles with 2 openings (biforous)
..... **Histeridae**
- 11(5). Body clothed with long, dense, erect, dark-coloured setae (Figs 28G, 33B) 12
Body clothed with numerous pale setae, or sparse setae, or without setae 13

- 12(11). Second segment of antenna longer than labrum is wide (Fig. 33B); mandible with a mola **Lagriidae**
 Second segment of antenna shorter than labrum is wide; mandible without a mola **Dermestidae**
- 13(11). One or more of the thoracic tergites with dark, sclerotized patches, smaller than the tergite 14
 Thoracic tergites without dark sclerotized patches (whole tergites sometimes dark, sclerotized) 22
- 14(13). Sensory process of antenna longer than the 3rd segment which bears a seta (larvae always less than 5 mm long; in woody fungi) **Ciidae**
 Sensory process of antenna not longer than the 3rd segment (larvae often more than 5 mm long) 15
- 15(14). Mandible with a penicillus (soft, setiferous process on inner face) **Phalacridae**
 Mandible without a penicillus 16
- 16(15). Labial palpi 1-segmented; body not coloured **Nitidulidae**
 Labial palpi 2- or 3-segmented; body often coloured, yellow, pink or blue 17
- 17(16). Sutures on the dorsal surface of the head V-, U- or lyre-shaped, coronal suture absent .. 18
 Sutures on the dorsal surface of the head Y-shaped, coronal suture obvious 21
- 18(17). Labrum not distinguishable; body clothed with numerous setae; epicranial suture lyre-shaped **Elateridae** (*Pseudotetralobus*)
 Labrum distinguishable; body usually with few setae; epicranial suture V- or U-shaped 19
- 19(18). All tergites with sclerotized areas; head with 6 stemmata on each side (on fledglings, in birds' nests) **Cavognathidae**
 With dark sclerotized areas only on the thoracic tergites; head with 5 or fewer stemmata on each side 20
- 20(19). Mandibles with 2 apical teeth; mentum and maxillary stipes very long; general body colour whitish **Trogossitidae**
 Mandibles with one apical tooth; mentum and maxillary stipes not elongate; general body colour often pink, yellow or blue **Cleridae**
- 21(17). Body with long, stout, branched spines borne on dark, sclerotized areas on each tergite; head hypognathous **Coccinellidae** (*Epilachna*)
 Body without long branched spines, often with numerous setae; head prognathous; body sometimes coloured orange or pink **Melyridae**
- 22(13). Spiracles unifornous (with a single opening), annular or elliptical 23
 Spiracles biforous 34
- 23(22). Prothorax swollen, much larger than the head and 2nd segment; body slender (Fig. 27G) **Lymexylidae**
 Prothorax not swollen, not larger than head and 2nd segment; body not unusually long and slender 24
- 24(23). Eighth abdominal tergite one-and-a-half or more times as long as 7th (Fig. 31H); body sometimes very strongly flattened; sometimes with head wider than prothorax **Cucujidae**
 Eighth abdominal tergite not or scarcely longer than 7th; body not unusually flattened; head not wider than the prothorax 25
- 25(24). Sutures on dorsal surface of head lyre-shaped or absent 26
 Sutures on dorsal surface of head U-, V- or Y-shaped 30
- 26(25). Mandible without a mola; body with dorsal surface roughened or with setiferous tubercles (in fungi) **Erotylidae**
 Mandible with a mola (e.g. Fig. 33G) 27
- 27(26). Labial palpi 1-segmented; without labrum (Fig. 30c) **Nitidulidae**
 Labial palpi 2-segmented; labrum visible 28

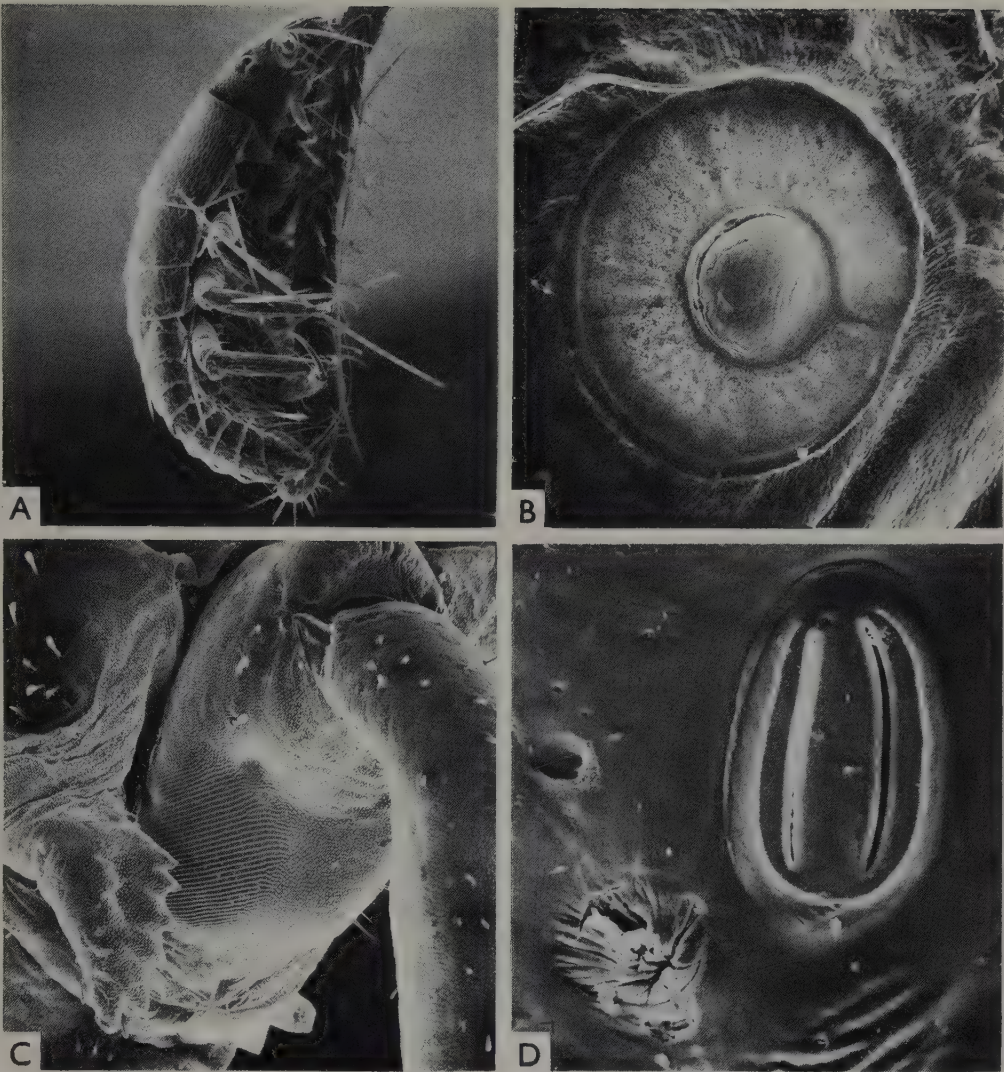


Fig. 26. A, Triungulin larva, Meloidae; B, cribriform spiracle of larva of *Anoplognathus montanus*, Scarabaeidae-Rutelinae; C, stridulatory file (on mid coxa) and scraper (modified hind leg) of larva of *Aulacocyclus* sp., Passalidae; D, biforous larval spiracle and scar of ecdysial tube, Elateridae.
[Scanning electron micrographs A–C by E. B. Britton, D by B. K. Filshie]

- 28(27). Mandible with an elongate, setose lobe at base on proximal side of mola; frontal sutures faint or absent; one stemma on each side of head **Anthicidae**
- Mandible without a setose lobe above the mola 29
- 29(28). Abdomen with pseudopods on the ventral side of segments 2–4 or 2–5 and transverse swellings covered with asperities (small spines) on the dorsal side of some anterior segments, apical abdominal processes simple, short, upcurved (in decaying wood) **Oedemeridae**
- Abdomen without ventral pseudopods or dorsal transverse swellings bearing asperities, but sometimes with roughened tubercles (in decaying vegetable matter, feeding on moulds) **Endomychidae**

- 30(25). With paired pseudopods on the ventral side of abdominal segments 2-4 or 2-5, and sometimes with 2 or more dorsal transverse swellings covered with asperities (in decaying wood) **Oedemeridae**
Without pseudopods or dorsal transverse swellings 31
- 31(30). Antennae with 2nd segment large, longer than labrum is wide (Fig. 33B), 3rd segment dome-shaped, minute, or absent; head hypognathous; body clothed with long, dense setae **Lagriidae**
Antennae clearly 3-segmented, 2nd segment not abnormally large; head prognathous or slightly inclined downwards; body not densely setose 32
- 32(31). Abdomen without longitudinal pleural sutures on each side **Pythidae**
Abdomen with longitudinal pleural sutures on each side 33
- 33(32). Length often more than 6 mm; mandible without a retinaculum **Tenebrionidae**
Length less than 6 mm; mandible with a long, slender retinaculum (Fig. 32H) attached on the inner face immediately distal to the mola **Cryptophagidae**
- 34(22). Without a labrum (Fig. 33A); mandible without a mola **Elateridae**
With a labrum; mandible with a mola 35
- 35(34). Labial palpi 1-segmented **Nitidulidae**
Labial palpi 2-segmented 36
- 36(35). Mandible with a long slender retinaculum (e.g. Fig. 32H) or a flexible penicillus attached to its inner face distal to the mola; body length less than 5 mm 37
Mandible without a long, slender retinaculum or penicillus 38
- 37(36). Mandible with a long, slender, rigid retinaculum arising from the inner face; maxillary mala falcate **Cryptophagidae**
Mandible with a slender, flexible penicillus arising from the inner face; maxillary mala rounded **Phalacridae**
- 38(36). Maxillary mala falcate or at least with an inwardly directed pointed apex 39
Maxillary mala rounded at the apex 40
- 39(38). Head with 6 stemmata on each side; all tergites with dark, sclerotized areas; mandible without a premolar tooth (on fledglings, in nests of birds) **Cavognathidae**
Head with 1 stemma on each side; tergites without dark sclerotized areas; mandible with a premolar tooth (stem-borers) **Languriidae**
- 40(38). Length less than 5 mm **Mycetophagidae**
Length often more than 5 mm **Zopheridae**
- 41(2). Thoracic legs 2-5-segmented 42
Thoracic legs minute, 1-segmented, or absent 94
- 42(41). Body C-, U- or J-shaped (e.g. Figs 30A, D, F, 31J); if C-shaped, the body occupies a quarter or more of the circumference of the projected circle 43
Body humped (i.e. dorsal curvature greater than ventral curvature—e.g. Figs 30B, C, 31E, F) or subparallel in lateral view, the curve of the ventral surface, if any, occupying much less than a quarter of the circumference of the projected circle 55
- 43(42). Spiracles crescent-shaped or kidney-shaped (Fig. 26B), cribriform (perforated like a sieve) 44
Spiracles not crescent-shaped or kidney-shaped, and not cribriform 48
- 44(43). Sutures on the dorsal surface of head V-shaped, arising from the occipital foramen; labrum almost hidden beneath the clypeus; abdomen with 10th and sometimes 9th segments vestigial **Dascillidae**
Sutures on the dorsal surface of head Y-shaped; labrum obvious; 10th abdominal segment well developed but sometimes fused with 9th 45
- 45(44). Antennae 4-segmented (e.g. Figs 32I, 33E) (often root-feeders) **Scarabaeidae**
Antennae 3-segmented (not root-feeders) 46

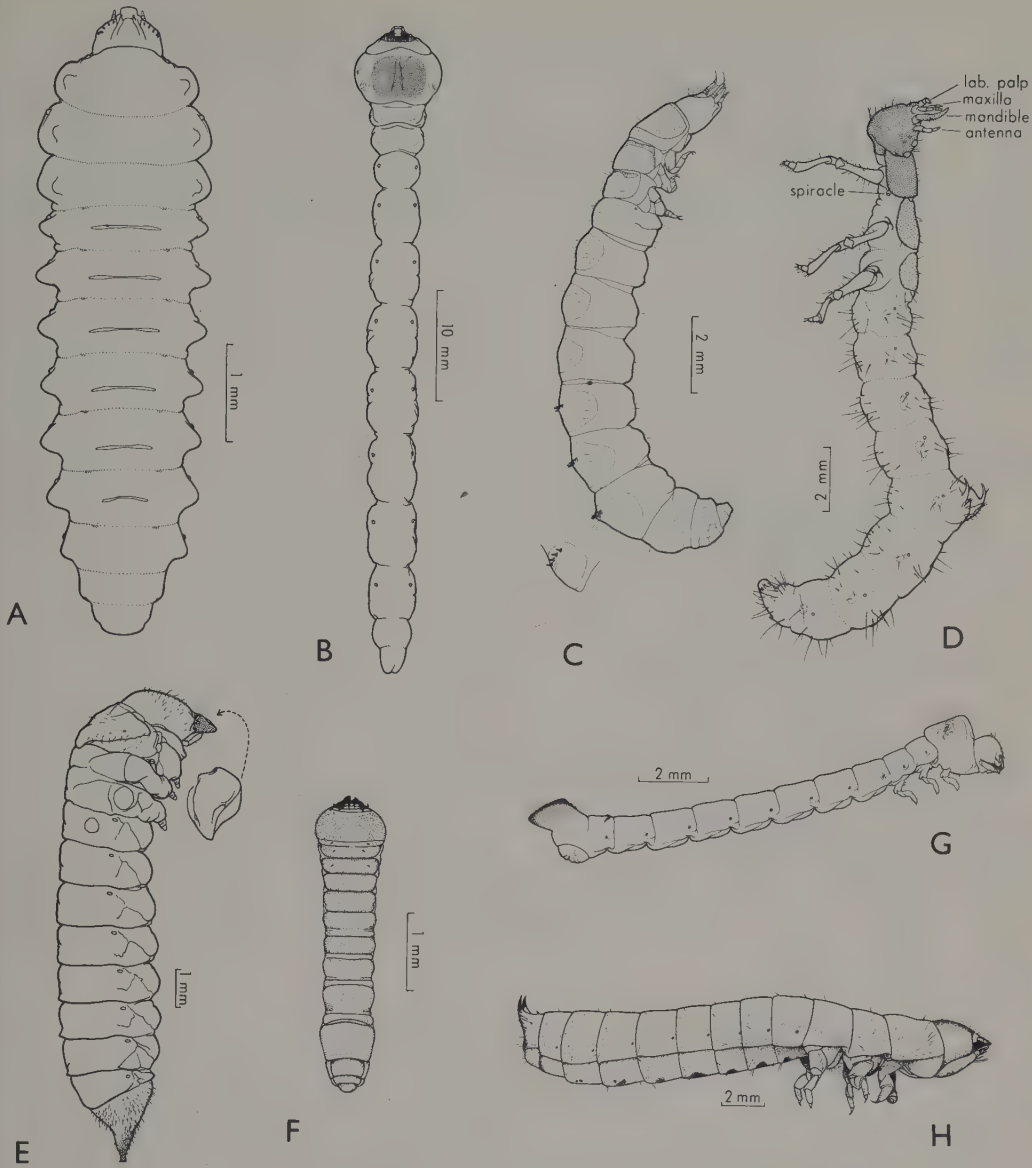


Fig. 27. Larvae: A, Chrysomelidae-Hispinae, *Uroplata girardi*, ventral; B, Buprestidae, dorsal; C, Carabidae-Pseudomorphae, *Sphallomorpha* sp.; D, Carabidae-Cicindelinae, *Cicindela* sp.; E, Mordellidae; F, Cerambycidae, ventral; G, Lymexylidae, *Melitomma pervagus*; H, Tenebrionidae, *Promethis nigra*.
[A, B, D, E, G by A. Klinkenberg; C by B. P. Moore]

- 46(45). Trochanter of hind leg and coxa of mid leg not modified for stridulation; abdominal tergites each with 3 transverse folds bearing conspicuous sharp setae and longer setae; head with stemmata near antennal bases (associated with carrion) **Trogidae**
- Trochanter of hind leg modified as a scraper which rubs over an area of fine ridges on the coxa of the mid leg; abdominal tergites without transverse folds; head without stemmata near the antennal bases 47

- 47(46). Body very strongly curved, obviously thickest in the middle and tapered to both ends; legs slender, without claws; hind legs sometimes reduced (in burrows in soil, not associated with decaying wood) **Geotrupidae**
 Body less sharply curved, not obviously thickened in the middle; legs strong, with at least a trace of claws on the fore legs (associated with decaying wood) **Lucanidae**
- 48(43). Larva J-shaped, living in a portable dark-coloured case, the entrance of which can be sealed by the head; head flat, heavily sclerotized, dark; pronotum also sclerotized and dark (Fig. 31I, J) **Chrysomelidae-Cryptocephalinae, Clytrinae**
 Larva not in a case 49
- 49(48). Spiracles biforous; maxilla with a well-developed lacinia 50
 Spiracles uniforous, annular, or slit-like; maxilla usually without a lacinia 51
- 50(49). Tergites sclerotized and pigmented; abdominal tergites without transverse folds; mandible without a mola (larvae in soil) **Byrrhidae**
 Tergites soft, not pigmented; abdominal tergites with transverse folds; mandible with a mola (associated with carrion) **Trogidae**
- 51(49). Head usually with 5 or 6 stemmata on each side; body usually pigmented; or, if pale and without stemmata, then found in soil feeding on roots **Chrysomelidae**
 Head with 1 or no stemma on each side; body white except for the mandibular region (feeding on dry wood or other dry materials, not in soil) 52
- 52(51). Head exserted, hypognathous (e.g. Fig. 30F); antennae minute or vestigial; setae on body abundant 53
 Head partly sunk into prothorax, usually prognathous; antennae larger, usually 3-segmented; few setae on body 54
- 53(52). Anterior spiracles situated on antero-lateral part of prothorax; abdominal tergites without transverse bands of spinules (never wood-borers, common species are pests of dry foodstuffs and museum specimens) **Ptinidae**
 Anterior spiracles situated on postero-lateral part of prothorax; abdominal tergites each with a transverse band of spinules (Fig. 30F) (almost always wood-borers, but *Stegobium paniceum* and *Lasioderma serricorne* are pests of dry, stored foodstuffs and plant materials) **Anobiidae**
- 54(52). Eighth abdominal spiracles of about the same size as the other spiracles (wood- and cane-borers, but *Rhyzopertha dominica* is a pest of stored wheat) **Bostrychidae**
 Eighth abdominal spiracles much larger than the other spiracles (wood-borers—'powder-post beetles') **Lyctidae**
- 55(42). Legs 5-segmented plus 1 or 2 claws 56
 Legs 2-4-segmented, with or without a claw 60
- 56(55). Labrum present; maxilla with both lacinia and galea (Fig. 33F); mandible with a mola; abdomen 9-segmented, the terminal segment conical (Fig. 28B) (feeding in rotting wood) **Cupedidae**
 Labrum absent; maxilla usually with galea only; mandible without a mola 57
- 57(56). Anterior edge of head with a median projection; labial palpi replaced by papillae; mentum and ligula fused into a single anteriorly bilobed piece; abdomen 10-segmented (in decaying wood) **Rhysodidae**
 Anterior edge of head without a median projection; labial palpi segmented; abdomen 8- or 10-segmented 58
- 58(57). Abdomen 8-segmented, without tergal hooks or spines; terminal segment discoidal, glandular (associated with ants) **Carabidae-Paussinae**
 Abdomen 10-segmented, with a pair of hooks on 5th tergite, or a transverse row of stout spines on each of the 5th, 6th and 7th tergites (living in a short burrow, predatory) 59
- 59(58). Fifth abdominal tergite bearing a pair of hooks (Fig. 27D) **Carabidae-Cicindelinae**
 Fifth, 6th and 7th abdominal tergites each bearing a transverse row of dark, short, stout spines (Fig. 27C) (in burrows close to ants' nests) **Carabidae-Pseudomorphae**

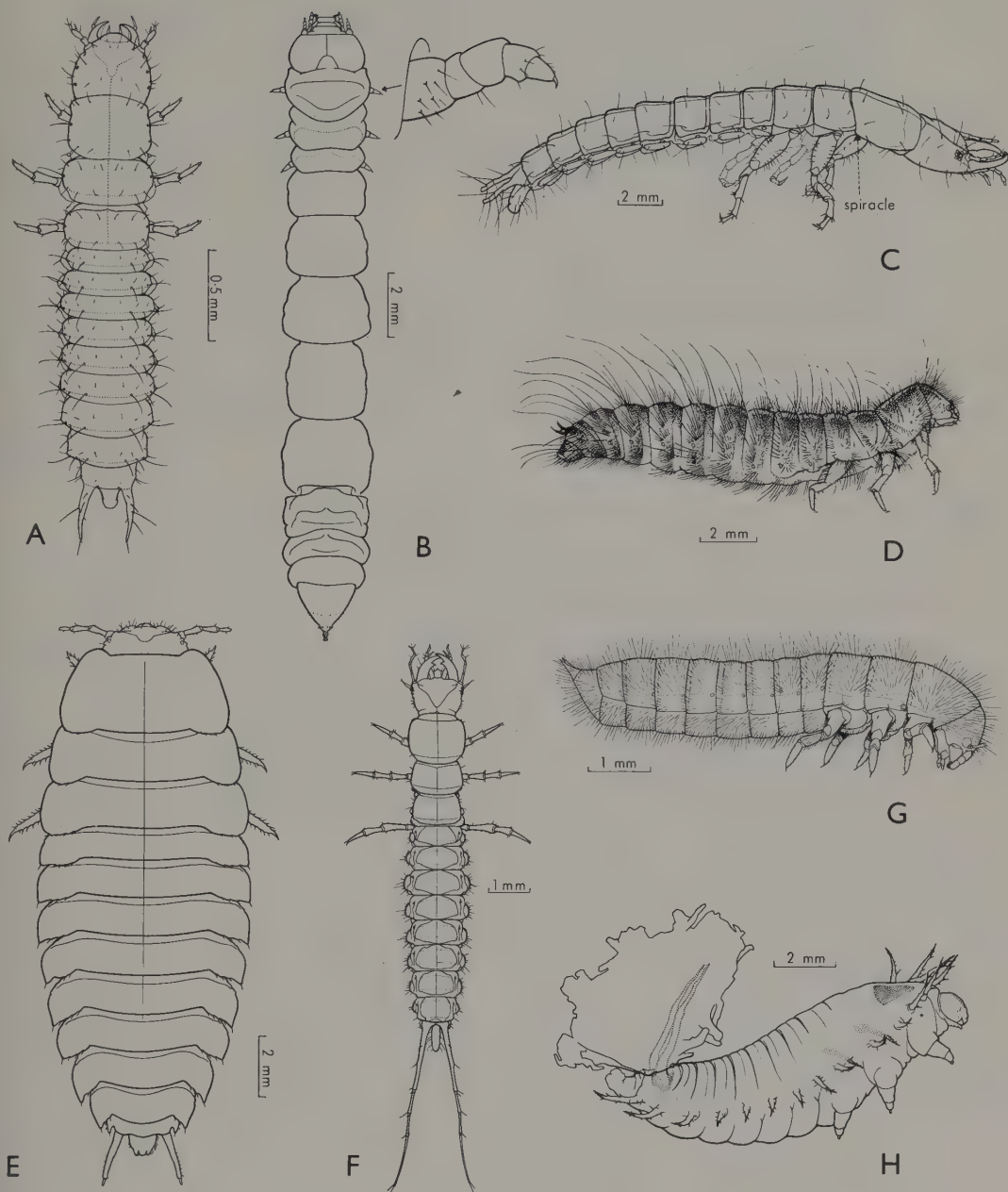


Fig. 28. Larvae: A, Staphylinidae-Omaliinae, *Omalius* sp., dorsal; B, Cupedidae, *Cupes varians*, dorsal; C, Carabidae-Broschinae, *Eurylychnus blagrovei*; D, Dermestidae, *Dermestes maculatus*; E, Silphidae, *Ptomaphila lacrymosa*, dorsal; F, Carabidae-Odacanthinae, *Eudalia macleayi*, dorsal; G, Lagriidae, *Lagria grandis*; H, Chrysomelidae-Cassidinae.

[A-C, E, H by A. Klinkenberg]

- 60(55). Mandible without a mola (e.g. Figs 32J, K, 27E) 61
 Mandible with a mola (e.g. Fig. 33G) 80
- 61(60). Mandible with the lower surface concave and the apex with 4 or 5 terminal teeth (e.g. Fig. 32J, K) 62
 Mandible sickle-shaped or triangular, if with lower surface concave then without a terminal row of teeth 63
- 62(61). Antenna 1-segmented; spiracles biforous; terminal segment (9th) of the abdomen in form of an operculum (parasitic on other insects) **Rhipiceridae**
 Antenna 2- or 3-segmented; spiracles annular; 9th abdominal segment not an operculum (plant-feeders) **Chrysomelidae**
- 63(61). Labrum absent 64
 Labrum distinct, separate from clypeus 69
- 64(63). Legs minute, 2-segmented; antennae minute, 1-segmented; head hypognathous; body cylindrical (wood-borers) **Brentidae**
 Legs obvious, 4-segmented; antennae 1-3-segmented; head usually prognathous; body usually flattened (if cylindrical, then prognathous) 65
- 65(64). Body wholly unpigmented; mandibles separated and non-functional; antennae 2-segmented and more than half as long as the front legs (termitophilous; Fig. 24) **Staphylinidae-Aleocharinae**
 Body pigmented; mandibles opposable, functional; antennae 1-3-segmented and very short 66
- 66(65). Antennae 1- or 2-segmented and unusually short and thick (Fig. 33D), the terminal segment conical, as broad as long; tergites heavily sclerotized, with lateral tubercles **Lycidae**
 Antennae 3-segmented, longer than wide (e.g. Fig. 33C); tergites not heavily sclerotized and without lateral tubercles 67
- 67(66). Body cylindrical, head exserted; epicranial sutures lyre-shaped (Fig. 33A) (in soil, decaying wood or vegetable matter, predatory) **Elateridae**
 Body more or less flattened, head retracted; epicranial sutures V-shaped or absent 68
- 68(67). Body and posterior part of head (Fig. 33C) dull, with velvety pubescence; tergites not laterally expanded; without luminous organs **Cantharidae**
 Body and posterior part of head not dull and velvety; tergites usually expanded laterally into horizontal flanges (Fig. 31C); sometimes with luminous organs **Lampyridae**
- 69(63). Legs minute, length of anterior legs less than one-fifth of the distance between their coxae 70
 Legs obvious, length of anterior legs more than one-fifth of the distance between them 72
- 70(69). Antennae minute, 1-segmented; legs minute, 2-segmented (wood-borers) **Brentidae**
 Antennae 2- or 3-segmented; legs 2- or 4-segmented 71
- 71(70). Prothorax wider than remainder of body (Fig. 27F); terminal segment of abdomen not conical (wood-borers) **Cerambycidae**
 Prothorax not wider than remainder of body; terminal segment of abdomen conical (Fig. 27E) (wood- or stem-borers) **Mordellidae**
- 72(69). Abdominal tergites each with 2 or 3 convex, transverse folds of uniform width; abdomen never ending in a point; body curved (in soil, feeding on roots) **Chrysomelidae-Eumolpinae**
 Abdominal tergites with not more than one distinct, convex, transverse fold; abdomen sometimes ending in a point; body straight or curved 73
- 73(72). Spiracles situated below a lateral longitudinal ridge which runs along the thorax and abdomen; lateral longitudinal suture very obvious; body dark-coloured, sclerotized **Tenebrionidae**
 Thorax and abdomen without a lateral longitudinal ridge running above the spiracles; without an obvious longitudinal suture 74

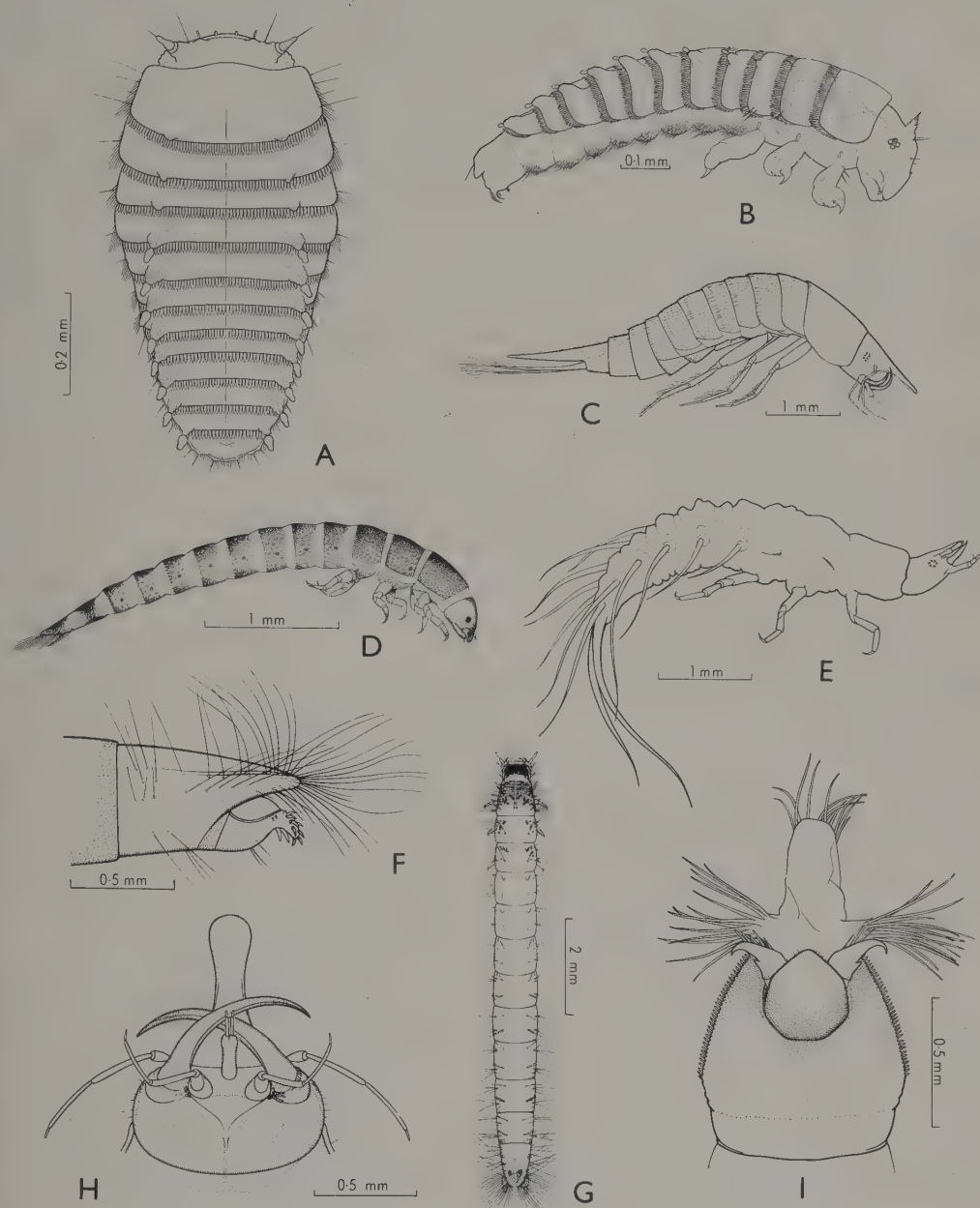


Fig. 29. Larvae: A, B, Sphaeriidae, *Sphaerius ovensensis*, dorsal, lateral; C, Dytiscidae-Hydroporinae; D, Helminthidae, *Austrolimnius waterhousei*; E, Hydrophilidae, *Berosus* sp.; F, G, Ptilodactylidae, caudal segment lateral, larva dorsal; H, Dytiscidae-Hydroporinae, head, ventral; I, Helminthidae, *Notriolus* sp., apex of abdomen, ventral to show operculum, hooks and extruded gills.

[B by E. B. Britton; E, I by A. Klinkenberg]

- 74(73). Body often densely clothed with setae (Fig. 28D), often with a dense bunch or bunches of setae at the caudal end, sometimes with specialized spear-headed setae; maxilla with both lacinia and galea present (often associated with dry animal remains—but *Trogoderma granarium* in grain) **Dermestidae**
 Body not densely clothed with setae, without bunches of setae at the caudal end, and without spear-headed setae; maxilla with a single lobe (except in Byrrhidae) 75
- 75(74). Terminal (8th) segment of the abdomen large, conical, at least as long as segments 4–7 together; abdominal segments with lateral tufts of setae; body heavily sclerotized and dark in colour **Nosodendridae**
 Abdomen with 9 or 10 segments; the terminal segment not unusually large 76
- 76(75). Body spindle-shaped, thickest in the middle (parasitic on larvae of Cerambycidae and Buprestidae) **Colydiidae-Bothriderinae**
 Body subcylindrical or with large, branched spines; not parasitic 77
- 77(76). Thoracic and abdominal segments with paired tubercles or dark sclerotized patches (Fig. 31D), with or without long, branched spines; maxilla with a single lobe (mala) **Coccinellidae**
 Thoracic and abdominal segments without paired tubercles, paired dark sclerotized patches, or long, branched spines; maxilla with one or two lobes 78
- 78(77). Maxilla with both galea and lacinia; terminal segment of abdomen without a conical or rounded process; tergites sclerotized and dark in colour **Byrrhidae**
 Maxilla with a single lobe (mala); terminal segment of abdomen produced into a conical or rounded process; body pale in colour 79
- 79(78). Ninth abdominal segment ending in a rounded process; head prognathous **Melandryidae**
 Ninth abdominal segment ending in a conical, pointed process; head hypognathous (Fig. 27E) **Mordellidae**
- 80(60). Spiracles crescent-shaped or kidney-shaped, cribriform (e.g. Fig. 26B); head without stemmata 81
 Spiracles circular or ovoid, not cribriform; head with stemmata 82
- 81(80). Metathoracic legs reduced to dentate stumps (Fig. 26C); antennae 2-segmented (Fig. 30E); concavity of the crescent of the prothoracic spiracles directed anteriorly, concavity of the crescent of other spiracles directed posteriorly; maxillary palpi 2-segmented (in rotting wood, always in association with adults; larvae walk with legs downwards) **Passalidae**
 Metathoracic legs fully developed (4 segments plus claw); antennae 3-segmented; concavity of the crescent of the prothoracic spiracle directed posteriorly, concavity of the crescent of other spiracles directed anteriorly; maxillary palpi 3-segmented (in decaying vegetation or rotting wood, not in association with adults; larvae walk on backs with legs upwards) **Scarabaeidae-Cetoniinae**
- 82(80). Body onisciform, <4 mm long; head not visible from above 83
 Body not onisciform, often more than 4 mm long; head visible from above 84
- 83(82). Body bearing numerous club- or fan-shaped setae; mouth-parts of biting type **Corylophidae**
 Body without club- or fan-shaped setae; mandibles and maxillae sometimes styliform, adapted for piercing **Cerylonidae**
- 84(82). Ninth abdominal segment longer than 8th, heavily sclerotized, and truncate (Fig. 27G) or pointed, with a bifurcate tip; prothorax larger than the mesothorax and swollen above the head (wood-borers) **Lymexylidae**
 Ninth abdominal segment usually shorter than 8th, if pointed then clothed with long setae and without bifurcate tip; prothorax not obviously larger and more swollen than the mesothorax 85
- 85(84). Epicranial suture Y-shaped, with a distinct coronal suture 86
 Epicranial suture U- or lyre-shaped, without a coronal suture 90

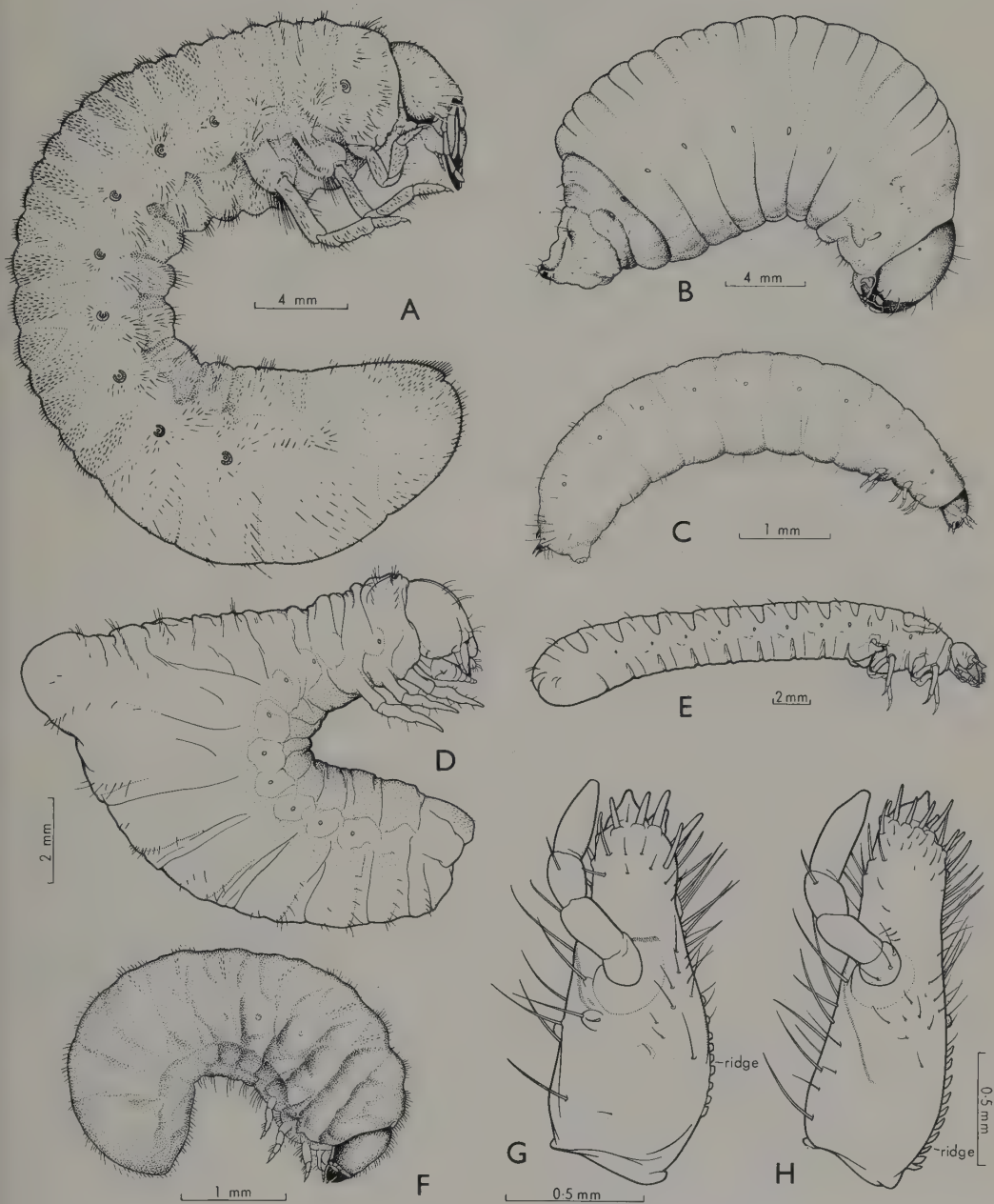


Fig. 30. Larvae: A, Scarabaeidae-Rutelinae, *Anoplognathus pindarus*; B, Curculionidae-Rhynchophorinae, *Trigonotarsus rugosus*; C, Nitidulidae, *Carpophilus hemipterus*; D, Scarabaeidae-Scarabaeinae, *Onthophagus gazella*; E, Passalidae, *Aulacocyclus* sp.; F, Anobiidae, *Stegobium paniceum*; G, Scarabaeidae-Dynastinae, *Heteronychus arator*, left maxilla, ventral; H, Scarabaeidae-Rutelinae, *Anoplognathus montanus*, left maxilla, ventral.
[A, D, E, G, H by A. Klinkenberg]

- 86(85). With dorsal ambulatory swellings on the posterior thoracic and anterior abdominal segments; sometimes with paired ventral pseudopods on anterior abdominal segments; prothoracic legs widely separated (Fig. 33G); anterior spiracles on prothorax (wood-borers) **Oedemeridae**
Without ambulatory swellings or ventral pseudopods; anterior spiracles on mesothorax 87
- 87(86). Antennae with 2nd segment large and thicker apically (Fig. 33B), 3rd segment minute or absent; body densely setose **Lagriidae**
Antennae 3- or 4-segmented; if 2nd segment is large, then 3rd is thinner but about as long as the basal segment 88
- 88(87). Mandible with upper and lateral faces meeting in a sharp, longitudinal ridge (Fig. 32E); 9th abdominal segment rounded and overlying the very reduced 10th segment which bears 2 small lobes (Fig. 32D) **Alleculidae**
Mandible without a lateral longitudinal ridge 89
- 89(88). Mandibles wholly sclerotized, with 1 or 2 apical teeth and without apical setae; abdomen usually with a ventro-lateral longitudinal suture below the spiracles **Tenebrionidae**
Mandibles usually partly membranous, with 2 long apical setae; abdomen without an obvious ventro-lateral longitudinal suture below the spiracles **Lathridiidae**
- 90(85). Labial palpi 1-segmented **Nitidulidae**
Labial palpi 2-segmented 91
- 91(90). Maxillary mala pointed (Fig. 32B) **Silvanidae**
Maxillary mala rounded 92
- 92(91). Abdomen with 9th segment about twice as long as 8th, tapered and clothed with long setae **Scaptiidae**
Abdomen with 9th segment about as long as 8th 93
- 93(92). Upper surface often with dark sclerotized areas bearing spines; maxilla with cardo and stipes fused **Coccinellidae**
Upper surface without discrete dark sclerotized areas; maxilla with separate stipes **Tenebrionidae**
- 94(41). Mouth-parts largely vestigial 95
Mouth-parts well developed, with opposable mandibles 96
- 95(94). Body thicker in middle, of leathery consistency; mandibles in form of fixed lobes (in soil, in association with egg-pods of Orthoptera or in bees' nests) late instar **Meloidae**
Body parallel-sided, not leathery; mandibles dentate externally **Eucnemidae**
- 96(94). Head prognathous or inclined upwards, often retracted into prothorax; prothorax often flattened and wider than remainder of body; body usually straight; abdominal tergites with or without transverse folds 97
Head hypognathous or partly so; prothorax not flattened and not obviously wider than remainder of body; body usually curved; with 2 or more transverse folds on each abdominal tergite 101
- 97(96). Body C-shaped or thicker in the middle; mandibles with rounded apices and no mola (usually in seeds of Leguminosae) **Bruchidae**
Body straight, never C-shaped 98
- 98(97). Maxillae wholly palp-like, longer than the mandibles; labrum absent; abdomen with only 8 visible tergites **Hydrophilidae-Sphaeridiinae**
Maxillae not palpiform, not as long as the mandibles; labrum present; abdomen with 9 or 10 visible tergites 99

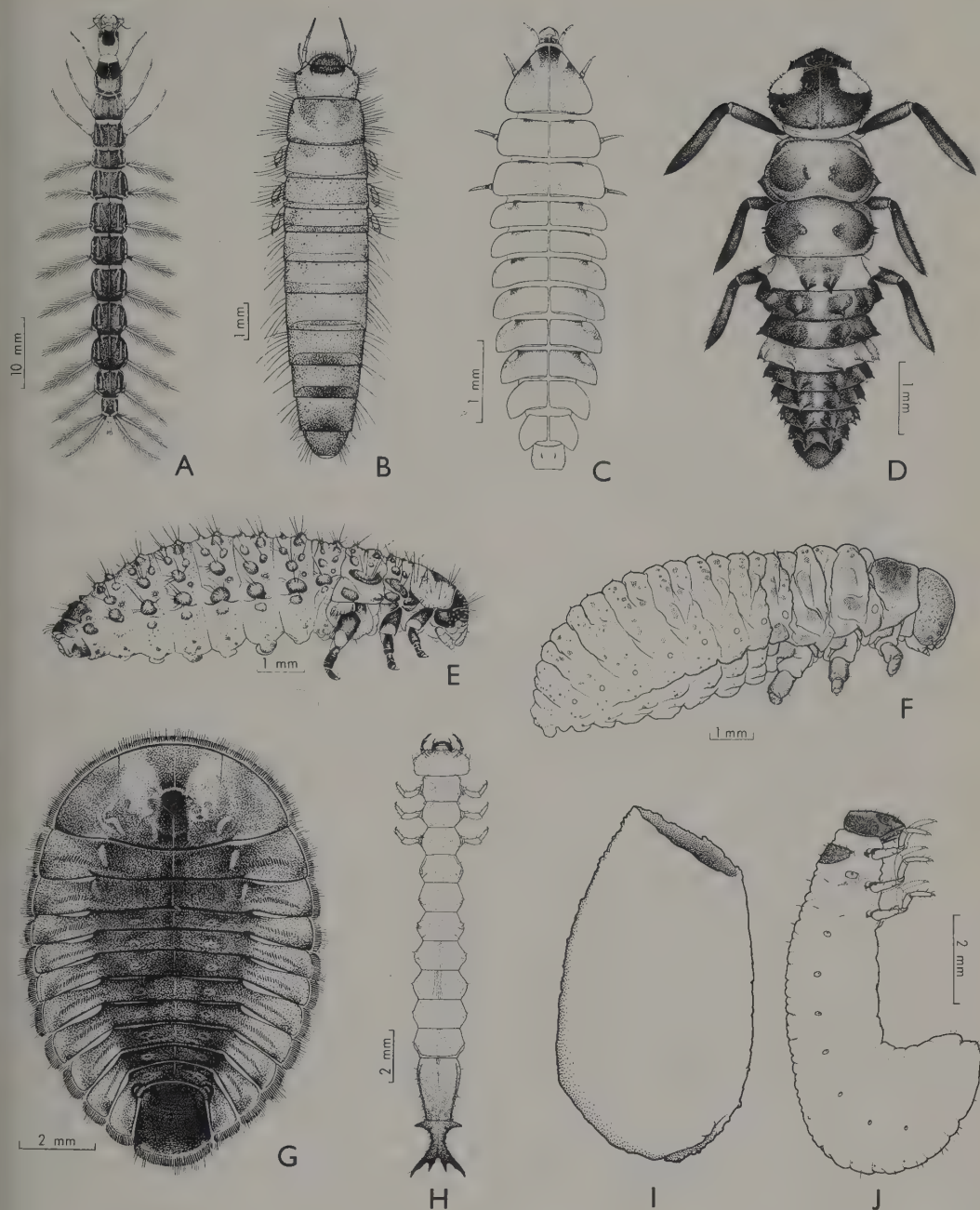


Fig. 31. Larvae: A, Gyrinidae, *Macrogyrus striolatus*, dorsal; B, Helodidae, dorsal; C, Lampyridae, *Luciola* sp., dorsal; D, Coccinellidae, *Coccinella repanda*, dorsal; E, Chrysomelidae-Chrysomelinae, *Paropsisterna beata*; F, Chrysomelidae-Criocerinae, *Crioceris nigripes*; G, Psephenidae, *Sclerocyphon* sp., dorsal; H, Cucujidae, *Platisus moerosus*, dorsal; I, J, Chrysomelidae-Cryptocephalinae, *Cryptocephalus parentheticus*, larval case and larva.

[F, I, J by A. Klinkenberg]

- 99(98). Labial palpi vestigial; stemmata absent; spiracles crescent-shaped or semicircular; prothorax obviously wider than rest of body and flattened (Fig. 27B) (wood-borers) **Buprestidae**
 Labial palpi 2- or 3-segmented; head with or without stemmata; spiracles oval; prothorax at most slightly wider than rest of body (borers in wood and stems, or leaf-miners) 100
- 100(99). Feeding on or in leaves; labial palpi 2-segmented; head with 5 or 6 eye-spots on each side (e.g. Fig. 27A) **Chrysomelidae-Hispinae**
 Feeding in wood or stems; labial palpi 3-segmented; head with 0-3 eye-spots on each side **Cerambycidae**
- 101(96). Ninth abdominal segment with a median caudal spine or conical process (Fig. 27E); thoracic legs vestigial **Mordellidae**
 Ninth abdominal segment without a pointed or conical process 102
- 102(101). Mandibles with a mola; maxilla with both galea and lacinia, the latter terminating in a curved spine **Anthribidae**
 Mandibles without a mola; maxilla with a single lobe 103
- 103(102). Body long, subcylindrical, slightly curved (wood-borers) **Brentidae**
 Body crescent-shaped, thicker in the middle than at ends; abdominal tergites each with 3 or 4 transverse folds (e.g. Fig. 30B) 104
- 104(103). Labial palpi unsegmented or absent (living in seeds) **Bruchidae**
 Labial palpi segmented **Curculionidae**
- 105(1). With thoracic legs 106
 Without thoracic legs 125
- 106(105). Legs 5-segmented plus 2 claws (except in Haliplidae which have 1 claw) **Suborder ADEPHAGA** 107
 Legs 4-segmented plus 1 claw **Suborders POLYPHAGA, MYXOPHAGA** 111
- 107(106). Filamentous lateral gills present on all abdominal segments; without spiracles; apex of abdomen bearing 4 hooks (Fig. 31A) **Gyrinidae**
 Abdomen without filamentous lateral gills on all segments; spiracles usually present; abdomen without apical hooks 108
- 108(107). Abdomen with 8 tergites visible from above 109
 Abdomen with 9 or 10 tergites visible from above 110
- 109(108). With slender, hair-fringed legs which are used for swimming; body widest in the middle, tapered to the posterior end; 8th abdominal segment usually long and pointed, often with long apical appendages (Fig. 29c); mandibles suctorial, with an internal duct and without teeth on the inner side (e.g. Fig. 29H) **Dytiscidae**
 With short, stout legs which are used for digging in mud or debris; body subcylindrical, not tapered, but with a short, pointed 8th segment and very short apical appendages; mandibles not suctorial, without a longitudinal duct or inner groove but with teeth on inner side near middle or base **Noteridae**
- 110(108). Each tarsus with one claw; abdomen 9- or 10-segmented; mandibles with a suction duct opening near the apex on the ventral side; head without epicranial sutures (feed on algae) **Haliplidae**
 Each tarsus with 2 claws; abdomen 9-segmented; mandibles without a suction-duct; head with epicranial sutures (e.g. Fig. 28F) (larvae among stones and gravel on river beaches, or under rocks in intertidal zone) **Carabidae**
- 111(106). Abdomen 8-segmented, with a small apical chamber containing 2 spiracles to which lead 2 stout parallel tracheal trunks, minute apical appendages, and small paired sclerotized processes; or segments 1-7 each with a pair of long simple tracheal gills; head often reflexed upwards at an angle to the body (Fig. 29E); maxillary palpi long, palpiform (Fig. 32c) **Hydrophilidae**
 Abdomen 9- or 10-segmented 112

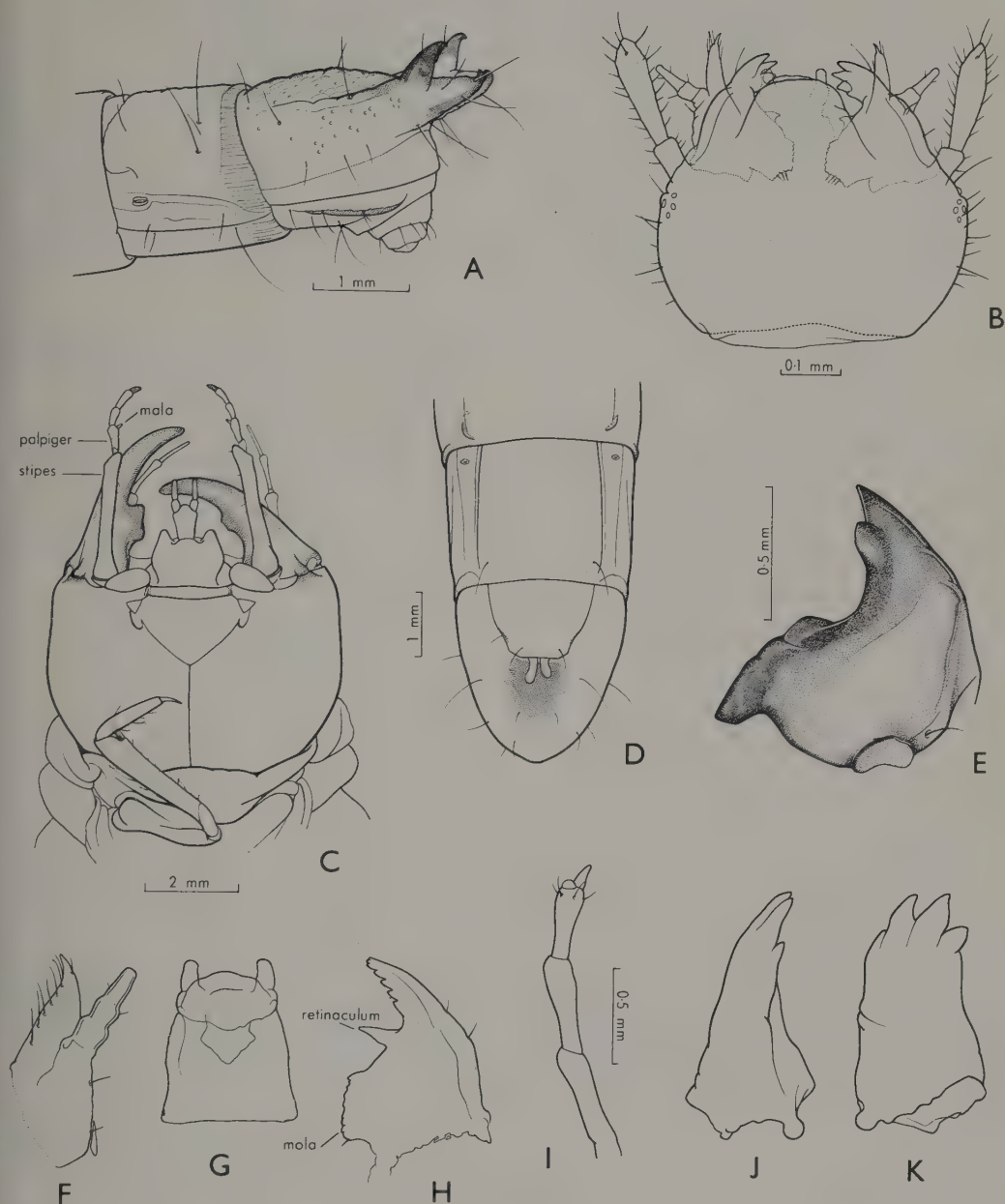


Fig. 32. Larvae: A, Elateridae, *Hapatesus hirtus*, caudal segments, lateral; B, Silvanidae, *Oryzaephilus surinamensis*, head, dorsal; C, Hydrophilidae, *Hydrous* sp., head, ventral; D, E, Alleculidae, *Tanychilus dubius*, caudal segments ventral, right mandible dorsal; F-H, Cryptophagidae, *Cryptophagus lycoperti*, right maxilla, labium, right mandible; I, Scarabaeidae-Aphodiinae, *Aphodius tasmaniae*, antenna; J, K, Chrysomelidae-Halticinae, *Haltica pagana*, right mandible, external and ventral.

[A. Klinkenberg]

- 112(111). Paired processes on 9th abdominal segment segmented or articulated to the tergite 113
 Paired processes on 9th abdominal segment not segmented, not movable, or apparently
 absent 114
- 113(112). Tenth abdominal segment with a pair of recurved hooks (length always less than 5 mm) **Hydraenidae**
 Tenth abdominal segment, if present, without hooks (length may be more than 5 mm) **Staphylinidae**
- 114(112). Antennae long, filiform, multisegmented (e.g. Fig. 31B); abdomen with retractable gills
 in a caudal chamber (in water, in tree-holes or very shallow water, especially water
 stained by iron bacteria) **Helodidae**
 Antennae short, at most 4-segmented 115
- 115(114). Body form greatly flattened, discoidal (Fig. 31G), the segments much expanded laterally
 (the larvae cling limpet-like to rocks in swiftly flowing streams) **Psephenidae**
 Body not discoidal 116
- 116(115). Abdomen with a pair of small spiracular gills or tubercles on each of segments 1-8
 (Fig. 29A, B); antennae 2-segmented; very small, length <2 mm (in wet mud and
 gravel at edges of streams) **Sphaeriidae**
 Abdomen without paired spiracular gills 117
- 117(116). Ninth abdominal segment with a ventral movable operculum (Fig. 29D) closing a
 caudal chamber containing extrudable gills (Fig. 29I) 118
 Ninth abdominal segment without an operculum 120
- 118(117). Operculum without hooks; head with 5 stemmata on each side (under rocks in inter-
 tidal zone, in tropics) **Limnichidae-Hyphalinae**
 Operculum with 2 hooks on its inner side (Fig. 29I) 119
- 119(118). Head with a single stemma on each side; thoracic sternites membranous; pleura dis-
 tinguishable on abdominal segments 1-4; 9th segment of abdomen distinctly longer
 than 8th (Fig. 29D) **Helminthidae (Elmidae)**
 Head with 5 stemmata on each side; thoracic sternites sclerotized; pleura distinguish-
 able on abdominal segments 1-6 or 8; 9th abdominal segment not longer than 8th
 **Limnichidae**
- 120(117). Abdomen with a pair of short sclerotized processes fused to the 9th segment 121
 Abdomen apparently without paired processes on 9th segment (or processes minute, at
 edge of a small apical chamber) 123
- 121(120). Head with 1 stemma on each side; thoracic tergites without dark, sclerotized areas **Anthicidae**
 Head with 3 or more stemmata on each side; pronotum sclerotized, dark in colour;
 meso- and metanotum each with 2 dark, sclerotized areas (in the intertidal zone) .. 122
- 122(121). Body, including tergites, bearing numerous, very long, fine, erect setae; abdomen with-
 out lateral pigment spots; head with 5 stemmata on each side **Melyridae (Dicranolaius)**
 Body with a few long erect setae arising from lateral pigmented spots or tubercles, with-
 out dorsal setae; head with 6 stemmata on each side (on sandy sea beaches) **Phycosecidae (Phycosecis)**
- 123(120). Ninth abdominal segment in the form of 2 stout conical lobes, each with recurved
 apices, terminated by a group of stout, brown spines (Fig. 29G, F); body cylindrical;
 head with a single pigmented eye-spot on each side **Ptilodactylidae**
 Ninth abdominal segment, if distinguishable, not in the form of 2 stout conical lobes
 with apical spines; body often tapered apically; head often with more than 1 pig-
 mented eye-spot on each side 124

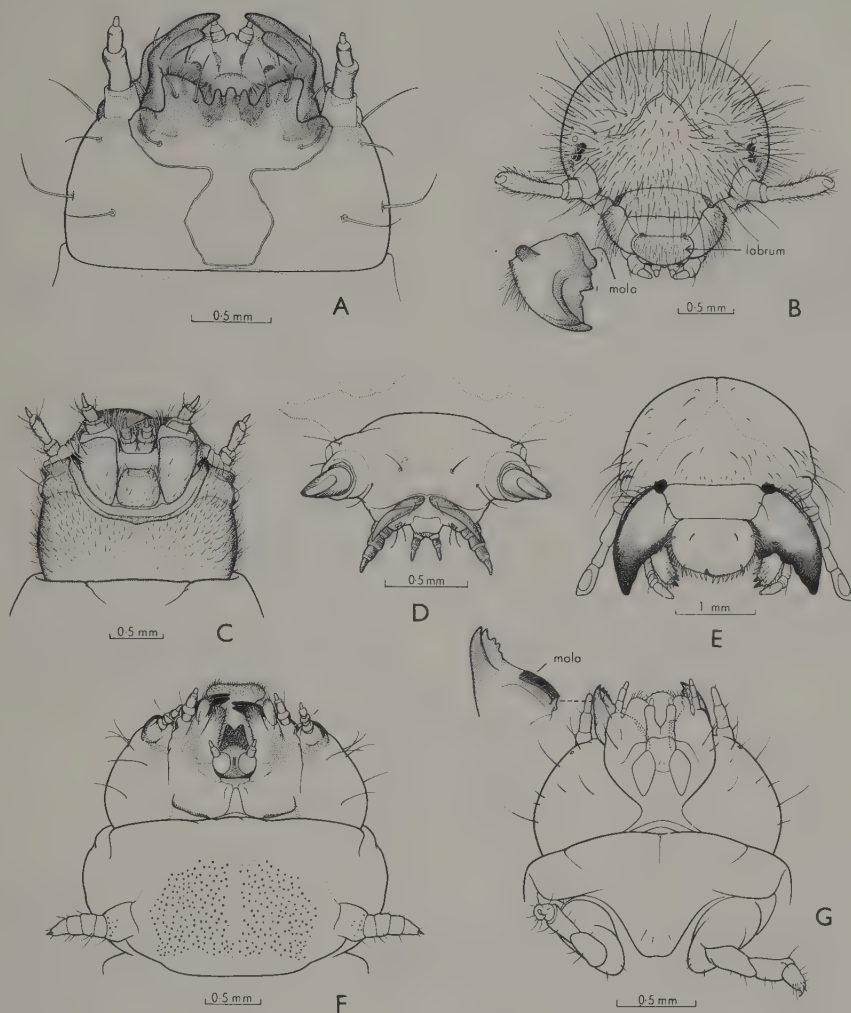


Fig. 33. Larvae: A, Elateridae, *Hapatesus hirtus*, head, dorsal; B, Lagriidae, *Lagria grandis*, head, anterior, and mandible; C, Cantharidae, *Chauliognathus pulchellus*, head, ventral; D, Lycidae, *Metriorrhynchus rhipidioides*, head, anterior; E, Scarabaeidae-Rutelinae, *Anoplognathus montanus*, head, anterior; F, Cupedidae, *Cupes varians*, head, ventral; G, Oedemeridae, head and mandible, ventral.

[A. Klinkenberg]

- 124(123). Abdomen with only 2 functional spiracles at end of 2 thick tracheal trunks which traverse abdomen, these spiracles large, inside a cavity at apex of the terminal segment (larvae surface to breathe); or (*Berosus*, Fig. 29E) with a pair of long filamentous tracheal gills on each of abdominal segments 1-7 (larvae permanently submerged); up to 30 mm in length **Hydrophilidae**
- Abdomen with functional spiracles on segments 1-8, without spiracles in a terminal cavity or filamentous tracheal gills (larvae in mud at edges of pools, etc.); small, <10 mm in length **Heteroceridae**
- 125(105). Mouth-parts directed forwards **Hydrophilidae** (*Cercyon*)
- Mouth-parts directed ventrally **Curculionidae** (*Bagous*)

STREPSIPTERA

by E. F. RIEK

Kinzelbach (1971a, b) has published two comprehensive monographs of the Strepsiptera of the world. He noted that the males are neoteinic in all features except those related to finding and inseminating the females, and concluded, partly because he could not homologize the fore wings with elytra, that the Strepsiptera are not beetles but a sister-

group of the Coleoptera. He proposed a new phylogenetic classification, in which the Mengenillidae are treated as a suborder Mengenillida and the remaining families in three superfamilies of Stylopodia, and described one new Australian species, *Coriophagus riei* (Halictophagidae), from a pentatomid bug.

MECOPTERA

(Scorpion-flies)

by E. F. RIEK

Hepburn (1969a, b) has studied the comparative morphology of the head and proventriculus, including representatives of all major Australian genera except *Austromerope*. Byers (1971) has pointed out that most adult Mecoptera are phytophagous, only the Bittacidae being predacious and the Panorpidae saprophagous, and that the mouth-parts show structural adaptations to the different feeding habits. Nygmata are present on the wings of all Australian genera studied (Fig. 32.5), although they were inadvertently omitted from Figure 32.1 and the text. Hepburn agreed with Byers (p. 644) in treating Apteropanorpidae as a family distinct from Panorpidae.

The larva of the New Zealand genus *Choristella* (Nannochoristidae) has been described by Pilgrim (1972). It is similar to

that of *Nannochorista* (Fig. 32.8) in structure, and was found, similarly, in fine silt at the bottom of shallow, quiet streams, where it feeds on chironomid larvae. It ceases to feed and leaves the water in the fourth instar, and usually makes a pupal cell in very damp soil or vegetation nearby. Nannochoristid larvae have also been found in an aquatic habitat in the Lower Cretaceous of Victoria, and wings comparable with those of modern species are known from the Upper Permian in New South Wales, so the family has clearly had a long history in what is now south-eastern Australia.

The **Choristidae** (3 genera, 8 spp.) have been revised by Riek (1973a). In **Bittacidae**, Smithers (1973b) has proposed a new monotypic genus *Tythobittacus* and described two new species of *Harpobittacus*.

SIPHONAPTERA

(Fleas)

by G. M. DUNNET

Major progress has been made in our knowledge of Australian fleas since the original chapter was written, so that many of the general statements now need modification and much of the taxonomy is out of date. Six new genera and over 30 new species have been described, and one species—*Spilopsyllus cuniculi* (Dale)—has been introduced from Europe to act as a vector of myxomatosis among rabbits. Several undescribed forms, including at least one new genus, still await study.

The situation up to the end of 1973 has been reviewed by Dunnet and Mardon (1974). This work contains keys, diagnoses

and illustrations of all described forms, together with host lists and maps for each species, a list of all fleas recorded from each host, and a bibliography of references to Australian material. A revision of the Stephanocircinae, with erection of a new genus *Coronapsylla* and description of 3 new species of *Stephanocircus*, was published by Traub and Dunnet (1973). Fleas are providing exciting new information about the biogeography of native rodents and marsupials, and, in particular, faunal links with New Guinea are becoming well illustrated from recent collections in northern Queensland.

DIPTERA

(Flies)

by D. H. COLLESS and D. K. McALPINE

In recent years considerable interest has developed in the comparative anatomy of Diptera and its implications for the higher classification of the order, in particular of the Schizophora (p. 94). Downes (1971) has also provided a useful perspective on the comparative ecology of blood-sucking groups. Our knowledge of fossil faunas, too, has been increased dramatically through studies by Quate (1961-3), J. F. McAlpine (listed in Griffiths, 1972) and Hennig (21 papers in

Stuttgarter Beiträge z. Naturkunde, 1964-8 and others to be cited below). This mass of new data and associated hypotheses may foreshadow considerable changes in our accepted classification of the order, but until that material has been carefully reviewed and digested, it would be premature for us to suggest any drastic amendments. However, we have made a few changes to the classification used previously, for reasons given at the appropriate places.

Fraenkel and Bhaskaran (1973) have provided a precise and useful terminology for the larva-adult transitional stages in Cyclorhapha, and Harrison's (1959) monograph of the New Zealand acalyptrate fauna should have been included in the faunal studies listed on p. 656. Also, an intensive survey of the regional fauna of western Arnhem Land was undertaken recently, the report (CSIRO, 1973) including accounts of the Diptera by Colless and by Standfast and Dyce. In the economic field, there have been important advances in knowledge of dung-breeding flies (p. 23), biting midges (Reye, 1971), and the arboviruses isolated from blood-sucking Diptera (Doherty *et al.*, 1973).

The known dipterous fauna has been increased by about 530 species, the approximate changes in the major divisions being:

Nematocera	from 1,836 to 2,052
Brachycera-Orthorrhapha	.. 1,811 .. 1,863
Brachycera-Cyclorrhapha	.. 2,609 .. 2,871

The greatest increases in individual families have been Psychodidae from 67 to 95, Chironomidae from 129 to 180, Scatopsidae from 21 to 57, Scenopinidae from 13 to 54, and Platystomatidae from 96 to 225.

Suborder NEMATOCERA

The **Tipulidae**-Tipulinae have been under detailed revision by Dobroworsky (see 1972; others to appear in *Aust. J. Zool.* Supplement series), and now include more than 150 Australian species. It has been found that at least some species of **Tanyderidae** have mandibulate mouth-parts of the blood-sucking type (Downes and Colless, 1967; Downes, 1971); their prey remains unknown. Duckhouse's (1966) review of the **Psychodidae**-Psychodinae brought our knowledge of the southern fauna up to date. Quate and Quate (1967) have recorded several tropical species that occur in New Guinea also, and study of our northern fauna will no doubt reveal many more in that category. Species of *Phlebotomus*, previously thought to be relatively uncommon, are now known to be widely distributed and quite common, particularly in

more arid areas (Dyce, 1971), and to harbour arboviruses (Doherty *et al.*, 1973).

Culicidae. Genetic and cytogenetic studies have shown that the common *Anopheles 'annulipes'* is a complex of at least two distinct biological species (Green, 1972). Marks (1970) has listed the Australian species of *Uranotaenia*.

Chironomidae-Podonominae were revised by Brundin (1966), who demonstrated extensive 'Antarctic' relationships between the faunas of the southern hemisphere. The previously reported chironomid with biting mouth-parts is now known (D. H. Edward, unpublished) to be a podonomine of the genus *Archaeochlus*, originally described from South Africa. Glover (1973) has reviewed the Tanytarsini, adding 33 new species to the previous 13. Jones (1974) has studied several Orthocladiinae that survive desiccation in the mud of dried out pools.

Ceratopogonidae. Debenham (1970-3) has reviewed 6 genera, 1 of them new and 2 not previously recorded in Australia. At least 4 show pronounced relationships with the Papuan fauna. A. L. Dyce (unpublished) has found increasing evidence that our species of *Culicoides* are much more widely distributed than hitherto believed; at least 4 range as far as Africa. Much practical information about *Culicoides* spp. is summarized in Reye (1971), while Kay (1973) has reported on the biology of the pest, *C. marmoratus* (Skuse).

Dumbleton (1972) has reviewed the classification and zoogeography of *Austrosimulium* and the general biology of **Simuliidae**, and, in **Blephariceridae**, P. Zwick (in preparation) has revised *Edwardsina*, clearing up synonymy and adding several new species. The **Perissommatidae** have been reviewed by Colless (1969). Discovery of the presumed larva of *Perissomma mcalpinei* leaves as diagnostic larval attributes only the reduced antennae, peripneustic tracheal system and short siphon with retractile spiracles.

A detailed review of **Scatopsidae** by Cook (1971) has revealed a normal and probably large fauna, dominated by *Colobostema* and *Rhegmoclema*; Aspitinae and Ectactiinae have not as yet been found in Australia. In

Cecidomyiidae, species of *Arthrocnodax* and *Lestodiplosis* have now been recognized in Australia, preying on orchard mites, also species of *Mycodiplosis* feeding on rust spores. Useful general works on the family have been published by K. Harris (1966, 1968) and Yukawa (1971). In **Mycetophilidae**, the glow-worm genus *Arachnocampa* has been reviewed by Harrison (1966), and the Ditomiyinae by Colless (1970).

Suborder BRACHYCERA

Division ORTHORRHAPHA

Athericidae. Stuckenberg (1973) has established this family, which differs from Rhagionidae, *inter alia*, in having a scale behind the metathoracic spiracle, a post-metacoxal bridge developed from the metepimera, cell R_1 of the wing closed at the margin, a pair of endophallic tines ('flagella') in the aedeagus of the male, and the cerci of the female 1-segmented. Athericidae agree with Tabanidae in all but the third of these features, but differ from them conspicuously in size and appearance and in having the antennal flagellum reduced to a single segment with a slender arista, cell R_1 closed, and squames very small and crumpled. The Australian genera are *Dasyomma* in the south and the almost cosmopolitan *Suragina* in north Queensland and New Guinea (Stuckenberg, personal communication).

Austroleptis (p. 701) should probably be removed also, to a family near Xylophagidae, so that Australian **Rhagionidae** will include only *Atherimorpha*, *Chrysopilus* and *Spaniopsis*. Three species of **Rachiceridae**, a specialized offshoot from Xylophagidae, have been described from New Guinea and New Britain by Nagatomi (1970), so *Rachicerus* may occur in northern Australia. In **Tabanidae**, the Australian species of *Tabanus* have been reviewed by I. Mackerras (1971); in **Stratiomyidae**, Nagatomi and Yukawa (1968) synonymized *Altermetoponia* with *Inopus*; in **Nemestrinidae**, Bernardi (1972) suggested removal of *Exeretoneura*, but offered no alternative

place for it; and in **Acroceridae**, Neboiss (1971) has revised the Panopinae.

Scenopinidae. The latest study by Kelsey (1971) brought the total of recently described species to 40, and it is now clear that the Australian fauna is large and distinctive, particularly in more arid areas. More than half the known species are so far represented by single specimens only, which suggests that a large fraction of the fauna remains to be discovered.

Bombyliidae. The family is badly in need of revision. A large amount of material is extant in collections, but probably less than half the fauna has been described. Hall (1969) reviewed the Cylleninae and revised *Thevenemyia*, and Bowden (1971a, b) has published on species in several genera.

Empididae. Hennig (1971b) suggested a revised classification of the subfamilies in relation to the Dolichopodidae, and K. Smith (1969) provided a useful, general account of the family and entry to the literature.

Division CYCLORRHAPHA

Series ASCHIZA

Ironomyiidae (Fig. 34A). J. McAlpine (1967, 1972) substantiated the claim of *Ironomyia* to family rank and, in the second paper, described a Nearctic species from Cretaceous amber. The family runs to Platyppezidae in the key on p. 701, but differs in having the second antennal segment with terminal processes on both inner and outer surfaces, Sc fused with R_1 for some distance but free apically, and M_2 arising from the apex of the discal cell.

In **Phoridae**, Borgmeier (1968, 1972) provided a full introduction to the literature, including recent studies of the Australian fauna. In **Syrphidae**, Vockeroth (1969) reviewed the Syrphini, including keys to Australian genera, and F. Thompson (1972) reviewed a number of tribes and proposed some drastic reclassification, including family status for *Microdon* and related genera. The acceptability of these proposals remains to be determined.

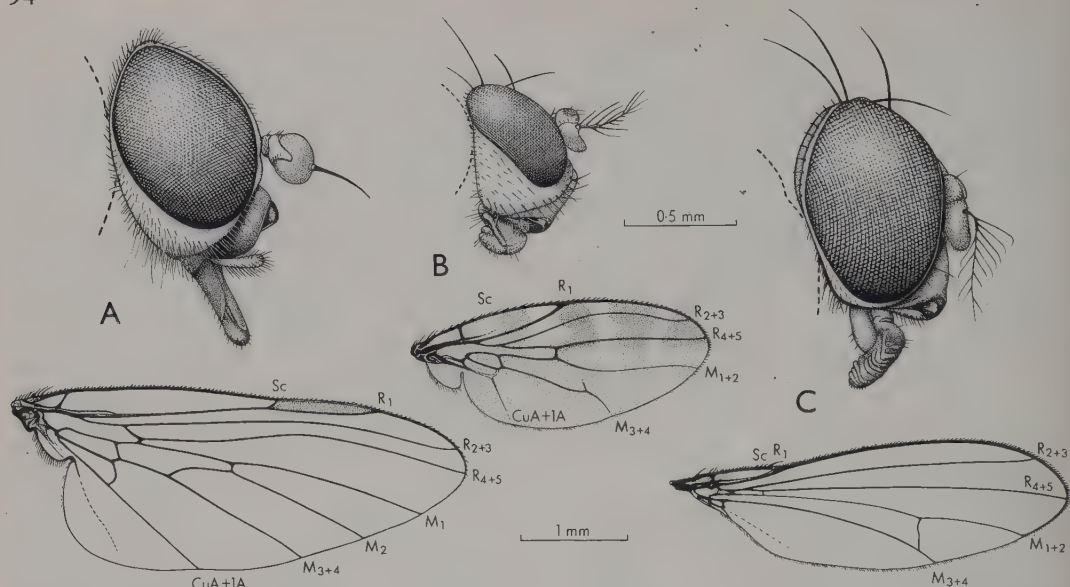


Fig. 34. A, *Ironomyia maculata*, Ironomyiidae; B, *Periscelis* sp., Periscelididae; C, *Axinota pictiventris*, Curtonotidae. [B. Rankin]

Series SCHIZOPHORA

In recent publications (Hennig, 1971a; Griffiths, 1972; Hori, 1967; Speight, 1969) many alterations have been made to the classification of Schizophora set out on p. 678. Among the more important changes that we recommend are the separation of Agromyzoidea (Carnidae, Odiniidae, Agromyzidae, Fergusoninidae) from Opomyzoidea, and of Chloropoidea (Tethinidae, Canaceidae, Milichiidae, Chloropidae, possibly Cryptochetidae) and Brauloidea (Braulidae) from Drosophiloidea; the removal of Lonchaeidae and Pallopteridae to the Tephritoidea and of Coelopidae to the Sciomyzoidea; and addition of Egniidae and Glossinidae to the Muscoidea.

The Tanypezoidea should perhaps include the Somatiidae and the recently established Neotropical Syringogastridae (Prado, 1969), to which the Papuan *Gobrya* (p. 722) may be related. In Sciomyzoidea, the Helcomyzidae should probably be merged with Coelopidae. Griffiths raised the Helosciomyzinae (p. 724) to family rank.

The Opomyzoidea are now restricted to the Neottiophilidae, Piophilidae, Opomyzi-

dae, Clusiidae and Acartophthalmidae, of which only Piophilidae and Clusiidae are known in Australia. Its limits are still uncertain. The first 3 families have the face divided by vertical sutures into three panels, and in the Opomyzidae the median panel is desclerotized; in Clusiidae the face is more broadly membranous. All the families have the postvertical bristles widely divergent, or sometimes absent, and the tarsi cylindrical or almost so.

The Agromyzoidea are less diffuse. They have generally incurved lower fronto-orbital bristles, divergent (sometimes parallel) postvertical bristles, distinct vibrissae, sclerotized face not divided as in Opomyzoidea, a more or less reduced subcosta, and the cerci of the female fused or joined by a membrane.

Hennig (1971a) recognized a superfamily Anthomyzoidea, roughly equivalent to our Asteioidea, but including also Acartophthalmidae, Clusiidae, Opomyzidae, Chyromyzidae and *Gayomyia* (p. 724). At present we prefer the more restricted limits, and use the name Asteioidea which has priority.

The Drosophiloidea are best distinguished from Chloropoidea (Milichioidea) on the structure of the antenna (Hennig, 1971a).

The third antennal segment of *Drosophiloida* has a basal dorsal tubercle fitting into a cavity in the second segment. The tubercle is absent in *Chloropoidea*, but present in several other families not often considered to be related, e.g. *Platystomatidae*, *Periscelididae*, and the presumed aulacigastrid genera *Cyamops* and *Stenomicroa*. The position of the *Cryptochetidae* remains doubtful. The relationships of the *Braulidae* (discussed by Hennig, 1938) have been so obscured by specialization that treatment as a separate superfamily involves the least confusion.

The sequence below follows the new arrangement.

Pseudopomyzidae. Hennig (1969a, 1971c) has contributed further to the systematics of the family and described a fossil from Oligocene amber.

Micropezidae. Australian genera formerly placed in *Calobatinae* are better included in a separate subfamily *Eurybatinae*; they include *Cothornobata*, *Crepidochetus* and *Metopochetus* (D. McAlpine, in preparation).

Eurychoromyiidae. This should, perhaps, be used as a family to include *Gayomyia*, but there is no general agreement on it (J. McAlpine, 1968; Hennig, 1971a). *Gayomyia* may be distinguished from Australian chamaemyiids by having vein CuA + 1A long and curved, R₁ with slight simple curvature distally, no narrow transverse swelling in front of scutellar suture, and shining black colour (our *Chamaemyiidae* are not shining and usually grey).

Lauxaniidae. A useful guide to world genera has been given by Stuckenberg (1971), but the generic assignment of many Australian species is still difficult. The *Celyphidae* probably do not merit separate family rank.

D. McAlpine (1967, 1968) has contributed to the systematics of the **Heleomyzidae**. The Australian **Sphaeroceridae** (O. Richards, 1973) include many introduced species of wide distribution. The subgenus *Leptocera* (*Biroina*), which is restricted to Australia and New Zealand, includes both winged and wingless species; the brachypterous *Otwayia* and apterous *Monteithiana* and *Bentrovata*

are endemic to Australia.

Numerous additional genera and species of **Pyrgotidae** have been collected, bringing the species total to over 90; the hymenopterous mimic *Eumorphomyia* occurs in north Queensland. In **Tephritidae**, the interesting wasp-like genera *Phytalmia* and *Diplochorda*, formerly placed in a family *Phytalmiidae*, have also been collected recently in north Queensland; the males have peculiar cheek processes.

Platystomatidae have been revised, in part, by D. McAlpine (1973). On present evidence the genus *Duomyia* (p. 721), with more than 70 species, is restricted to Australia. *Lenophila* is also endemic. The early stages of *L. dentipes* (Macq.) are evidently associated with *Eucalyptus*, but adults of the other 5 species are generally found on leaves of *Xanthorrhoea* and in 3 of them the larvae are known to live in the trunk of the plant.

In **Piophilidae** (= *Thyreophoridae*), further information on the genera has been given by Steyskal (1973).

Carnidae have the cerci of the female fused or joined by a membrane and the two spermathecae have complex sclerotized vesicles (Hennig, 1972); these are further points of distinction from *Milichiidae*. Griffiths (1972) proposed a separate family for *Australimyza*, but our studies tend to confirm its position in the *Carnidae*.

Hennig (1969a) provided a key to genera of **Odiniidae**. The Australian species, all rare in collections, belong, one each, in *Odinia*, *Traginops* and an apparently undescribed genus. A second genus of **Fergusoninidae** with large antennae not sunk into the facial cavities has been found in north Queensland, but its host plant is unknown.

Of the genera occurring in Australia, only the widely distributed, Old World, tropical *Amygdalops* remains in **Anthomyzidae**, and it would run out in couplet 52 of the key on p. 718. *Cyamops* and *Stenomicroa* were transferred to the **Aulacigastridae** by Hennig (1969a, 1971a), though their antennal structure is anomalous, and an undescribed Australian genus may also belong to this

family. Still another genus, considered to represent a new family, is associated with *Alocasia* in all stages, the larvae living among the developing fruitlets. It is related to an undescribed genus in southern Africa, and the Oligocene *Anthoclusia* could be the ancestor of both. Some Aulacigastridae would run to couplet 46, replacing Anthomyzidae there, and others to couplet 52, where they may be distinguished from *Amygdalops* by having only one strong fronto-orbital bristle, with a small setula close in front of it, and face entirely sclerotized, with median prominence bearing vibrissae below its summit. The remainder would run to the first half of couplet 29 (p. 717), and may then be separated by the following couplet.

- Ocellar bristles absent; Rs without bristles;
1 or 2 rows of acrostichal hairs or setulae
..... **Aulacigastridae** (pt)
- Ocellar bristles present; Rs with 3 strong
bristles dorsally towards base; mesonotum
with numerous non-seriate hairs
- undescribed genus near *Anthoclusia*

Periscelididae (Fig. 34B). A species of *Periscelis* has been collected recently in New South Wales and Queensland. It would run to couplet 52 (above), where it may be recognized by being a small broad fly (the others are slender) with broad wing, r-m and termination of R_1 near or beyond the middle, costa without trace of break or flexure, and cell M distinctly enclosed.

Asteiidae. A peculiar, primitive species recently found on Lord Howe Island has 3 reclinate fronto-orbital bristles and vein $CuA+1A$ distinct but veins enclosing cell CuP obsolescent; the wing is otherwise rather like that of *Leiomyza* (Fig. 34.32B). It has much in common with the Oligocene *Succinasteia* (Hennig, 1969b).

Curtonotidae (Fig. 34C). *Axinota pictiventris* Wulp from north Queensland, noted on p. 729, remains the only Australian representative of the family.

The classification of the **Muscidae** was treated by Hennig (1965), and Australian muscids have been further studied by Pont (1969a, b, 1972, 1973a, b). *Neohelina*,

which represents the **Eginiidae** in Australia, differs from the muscid genera among which it had been included by having the costa extending only to R_{4+5} (Pont, personal communication). Typical eginiids have a series of bristles on the mesopleuron and costa extending to M_1 , which is not bent forward distally.

Calliphoridae. Kurahashi (1971) has reviewed the genus *Calliphora*, and Norris (1973) has drawn attention to some important features of nomenclature in that genus. P. Ferrar (unpublished) has found that several species of *Ameniinae* develop single larvae, which are 'nursed' *in utero* to an advanced stage of development. The same phenomenon is known to occur in the striking *Euphumosia papua* (Guérin), an exceedingly common species in Arnhem Land (Colless, in CSIRO, 1973).

Sarcophagidae. It is now known that *Parasarcophaga knabi* (Parker) breeds commonly, and apparently preferentially, in animal faeces, and its larvae form a significant element of the dung fauna (L. T. Woolcock, unpublished). The species occurs also in Oceania and the Oriental Region.

Tachinidae. A major advance has been the comprehensive study of the Rutiliini by Crosskey (1973a) which, for the first time, places a major group of our tachinids on a sound taxonomic basis. The vast array in other tribes, however, continues to pose an immense problem, particularly in view of heightened interest in their potential for control of pests. In the *Anagonia-Froggattimyia* complex, for instance, parasites of leaf-eating sawflies and chrysomelid beetles, there are more than 30 species and fewer than 10 valid names. A rare, perhaps unique, instance of a tachinid parasitizing other Diptera has been reported by Spratt and Wolf (1972), who reared *Bactromyiella* sp. nr *ficta* (Walk.) from adults of 2 species of *Dasybasis* (Tabanidae). Since the above was written, Crosskey (1973b) has published a catalogue of Australian Tachinidae, with keys to genera and host lists.

The taxonomy, biology, and zoogeography of our **Streblidae** and **Nycteribiidae** were comprehensively reviewed by Maa (1971).

TRICHOPTERA

(Caddis-flies, caddises)

by E. F. RIEK

The reduced, sucking mouth-parts of adult Trichoptera were described on p. 741, but not illustrated. They are shown here in Fig. 35, with the characteristic haustellum which is developed from the hypopharynx, not from the galeae as in Lepidoptera or the labium as in Diptera.

H. Ross (1967) has reviewed the classification of the order, which he divided into 2 suborders, not equivalent to the old Aequipalpia and Inaequipalpia, namely: ANNULIPALPIA, adults with terminal segment of maxillary palp annulate (Fig. 35B), larvae in silken shelters (Hydropsychoidea with 7 families, 4 in Australia); and INTEGRIPALPIA, terminal segment of maxillary palp not annulate (Fig. 35A), larvae free-living or in saddle, purse or tube cases (Rhyacophiloidea with 3 families, all in Australia, and Limnephiloidea with 24 families, 15 in Australia). He treated

Glossosomatidae as a separate family in Rhyacophiloidea, and proposed 4 new families (Rhynchopsychidae, Calocidae, Pycnocentrellidae, Antipodoeciidae) and a new subfamily (Sericostomatidae-Conoesucinae) for Australasian limnephiloids, but the Conoesucinae should be referred to the Limnephilidae. Riek (1968b), however, in establishing the family Tasimiidae (p. 759), interpreted the Limnephiloidea to include only 8 families of case-makers which are characterized, *inter alia*, by lacking a lateral row of spicules on abdominal segment 8 of the larva; these correspond to the first section of the superfamily (descendants of 'ancestor 9') of Ross. Schmid (1969) transferred the mostly large, ornate, day-flying *Stenopsychodes* (p. 757) to the Stenopsychidae, even though they lack ocelli, adding this family to the Australian list.

It is evident that much work remains to be

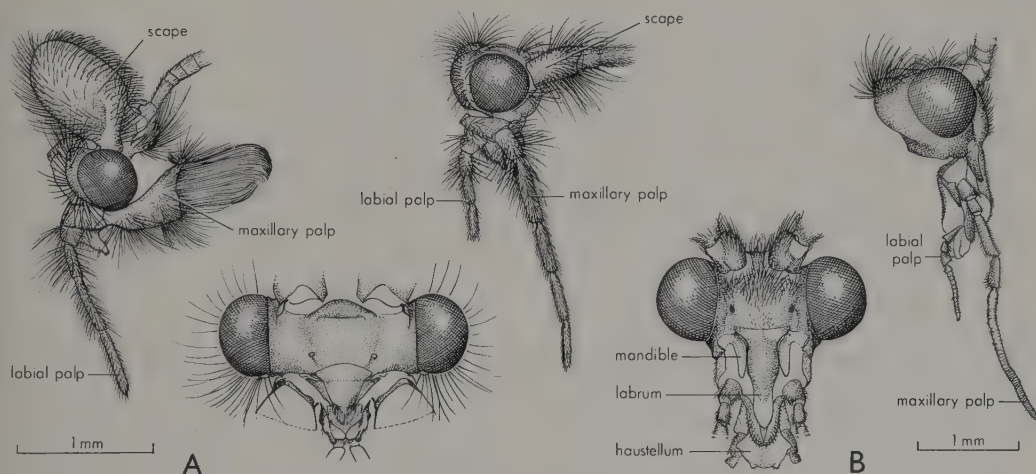


Fig. 35. Heads of: A, *Caenota* sp., Integrupalpia-Sericostomatidae, ♂ lateral, ♀ lateral, ♂ frontal; B, *Stenopsychodes* sp., Annulipalpia-Stenopsychidae, ♂.

[S. Monteith]

done on Australian Trichoptera. Nevertheless the studies reported above and extensive collections recently made in Chile by Dr O. Flint and in Tasmania by Mr A. Neboiss have shown that trans-Antarctic relationships in the order are stronger than had been indicated by earlier work. Those noted by

Ross (1967) include *Smicridea* in Hydropsychidae, Hydrobiosinae, Rhynchopsychidae, Philorheithridae, Leptoceridae-Triplectidinae, and there are others still unpublished. On the other hand, the marine Philanisidae are still known only from Australia and New Zealand and appear to have evolved locally.

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LEPIDOPTERA

(*Moths and butterflies*)

by I. F. B. COMMON

Several significant studies of the morphology, biology and phylogeny of the Lepidoptera have been reported recently. Of special phylogenetic significance is the work of Kristensen (1968a-c, 1971) on the anatomy of the adult head and alimentary canal in Zeugloptera and Dacnonypha, of Common (1973) on the comparative morphology of adult Dacnonypha, of Mutuura (1972) and Dugdale (1974) on the female genitalia in the primitive lepidopterous families, and of Brock (1971) and Hessel (1969) on the morphology of the thorax and dorsal vessel in adult Ditrysia. However, further comparative work is required, not only on the adults, but on larvae and pupae. It is unfortunate, for example, that no major comparative study of lepidopterous pupae has been undertaken since the classical studies of Mosher in 1916. A wealth of information has appeared in recent years on the physiology and behaviour of Lepidoptera, especially on sex attractants, courtship and mating, flight, feeding and nutrition, and sound production and perception, and some of this is touched on later.

Anatomy of Adult

Head. The presence or absence of a pair of ocelli has long been a useful character in the suprageneric classification of the Lepidoptera. However, Dickens and Eaton (1973) discovered that adults of some families, previously thought to be without ocelli, have in fact a pair of minute 'external ocelli' much more dorsally placed on the head than normal ocelli and covered by the scales. In these species there are corresponding 'internal ocelli', each connected to the brain by an ocellar nerve. In some species at least, a nerve branch runs from the internal to the external ocellus. The minute external ocelli were observed in species of the 5 families of Papilionoidea, and in the HesperIIDae, SaturnIIDae, SphingIDae and ArctIIDae-Lithosiinae. They may be homologous with the very minute papillae occurring on each side of the occiput in *Hepialus*, observed by Jordan in 1923. Hinton, in 1946, stated that the ocellar nerve persists with these organs, but the pigment and lens have been lost. He considered that they were not photoreceptors, and Jordan had suggested that they

were probably not homologous with the chaetosemata (p. 765).

Kristensen (1968c) showed that the coilable and functional haustellum in *Eriocrania* lacks intrinsic muscles, and extension of the haustellum in this genus must be effected by blood pressure. Hepburn (1971), in a detailed study of the extension-recoil cycle of the haustellum in Lepidoptera, concluded that elasticity, musculature and hydrostatic pressure all play a part, but the role of each must vary from one species to the next. Although the labial palps of *Sabatinca* and *Agathiphaga* are said to be 4-segmented, Kristensen (1967) pointed out that in these genera the basal 'segment' is probably only a part of the prementum, and the palps are therefore 3-segmented.

Legs. The function of the basally articulated epiphysis of the fore tibia (p. 767) found in most Lepidoptera has previously been a subject for speculation. In an experimental study Callahan and Carlisle (1971) showed that in *Heliothis zea* (Noctuidae) it is used to clean the antennae, even during flight.

Wings. Common (1969a) drew attention to the presence of an elliptical area of minute curved spines on the lower surface near the anal angle of the fore wing in many families of Lepidoptera. When the wings are closed these spines interlock with an area of similar spines on the metascutum, thus ensuring that the wings are folded in a precise position. The presence of this wing-locking mechanism is fairly well correlated with the method of wing-folding, and those families that fold their wings in the primitive roofwise position have both alar and thoracic structures well developed. Thus it occurs throughout the Zeugloptera, Dacnonypha and Monotrysis and in many superfamilies of the Ditrysis. However, both zones of spines are absent in the pyraloid families Thyrididae, Tineodidae and Oxychirotidae, and in the Pterophoroidea, most Geometroidea, Calliduloidea, Hesperioidea, Papilionoidea, Sphingoidea, and the Bombycoidea except the Lasiocampidae. In repose many of these groups hold their wings in various modified postures,

either partially spread or back-to-back above the body. Despite the modified resting postures of many Pyralidae, the spined zones have been retained throughout the family except in the Epipaschiinae. They are also present throughout the Notodontoidea and Noctuoidea, including those broad-winged Catocalinae and Ophiderinae that rest with wings outspread.

Abdomen. The abdominal tympanal organs of *Plodia* and *Ephestia* (Pyralidae) have been described by Mullen and Tsao (1971) and compared with those of *Galleria*. They were found to be less complex than the thoracic tympanal organs of Noctuidae. Each tympanum consists of only one chamber, and the tympanic membrane is divided into two parts, a taut, transparent tympanic membrane proper and a translucent counter-tympanic membrane. The chordotonal sensilla lead from the tympanic membrane proper, which detects sound waves, to the rear of the tympanic chamber and thence to the metathoracic ganglion.

The adult males of many Lepidoptera have eversible tufts or pencils of hairs, some of which are known to disseminate pheromones used during courtship. In Danainae a pair of hair pencils, extruded from the tip of the abdomen, dusts pheromone particles on to the antennae of the female during a courtship flight. Many Noctuidae have paired brushes of hairs in special pockets near the base of the abdomen which, when everted, disseminate pheromones produced by glands within the pockets and by Stobbe's glands in abdominal segment 2 (Birch, 1970).

Female reproductive organs. Mutuura (1972) found that the position of the genital apertures of several of the more primitive families of Lepidoptera is more diverse than was previously supposed. In groups with a single terminal genital aperture, its position varied from the end of abdominal segment 10 in Zeugloptera to the end of sternum 8 in Eriocraniidae, Adelidae and Heliozelidae. He indicated that the females of *Neopseustis* have separate genital and copulatory apertures, and that the external genitalia of *Neopseustis*, and probably

Mnesarchaea, are similar to those of Hepialidae. In *Mnesarchaea* the exoporian condition of the genitalia has been demonstrated by Dugdale (1974). Strong evidence is thus provided for removing the Neopseustidae and Mnesarchaeidae from the Dacnonypha to a position close to the Hepialoidea, and Dugdale regarded all three groups as primitive Ditrysia. Additional evidence for the relationship of *Neopseustis* to the Hepialoidea was given by Mutuura, who pointed out similarities in the male genitalia of *Neopseustis* and *Prototheora*.

The Tischeriidae were claimed by Mutuura to have two genital apertures, and so might occupy a position transitional between forms with one and two genital apertures. This has been discounted by Dugdale, who has shown that there is but a single genital aperture in *Tischeria* posterior to sternum 8 and that the Tischeriidae fit naturally into the Nepticuloidea.

As modifications in the morphology of the female terminalia are usually correlated with mode of oviposition, Mutuura placed great reliance on the latter in discussing the higher classification of the Lepidoptera. However, modes of oviposition and the associated structural modifications are so clearly adaptive that phylogenetic conclusions based only on such characters must be treated with caution. Unfortunately, Mutuura did not deal adequately with the disposition of the internal genital organs, which are less subject to change and therefore likely to provide more reliable indications of phylogeny.

Biology

Some Lepidoptera feed at dung, carrion, urine, fermenting juices, and the honey-dew produced by aphids and coccids, and must therefore ingest nutrients other than carbohydrates (Downes, 1973). A few tropical Pyralidae, Noctuidae and Geometridae have been reported feeding at the secretions of vertebrate eyes (Büttiker, 1967), and other species are capable of puncturing human skin with the haustellum to ingest blood (Bänziger, 1968). Baker and Baker (1973) have shown

that the nectar of many flowers at which adult Lepidoptera and other insects feed contains significant concentrations of a wide range of amino acids, which must contribute to its nutritional value. *Heliconius* butterflies supplement their nectar diet by collecting pollen grains, mixing them with nectar in the coils of the haustellum, and ingesting the amino acids that diffuse from them. Certain pollens release protein and free amino acids into sucrose solutions within a few minutes, so that enzyme digestion of the pollen proteins by the insect is not necessary. Experiments suggested that the amino acids ingested are of major significance in adult maintenance and reproductive capacity (L. E. Gilbert, 1972).

Many Lepidoptera are able to produce sounds, both sonic and ultrasonic. The clearly audible 'whistling' produced by the males of some Agaristidae such as *Hecatesia* and *Idalima* (p. 866) have long been known, and presumably have a function in bringing the sexes together. Less noticeable but nevertheless audible sounds have been reported in the cossid *Xyleutes* (Common, 1969a), Nymphalidae such as *Polyura*, and the sphingids *Acherontia* and *Psilogramma*. In the Palaearctic genus *Acherontia* a 'squeaking' sound is produced by air drawn in and expelled through the haustellum, whereas in *Psilogramma* stridulatory sounds are produced by a series of lateral movements of the external male genitalia, during which clusters of special scales on the valvae are rubbed on a comb of spines on the posterior margin of tergum 8. It has been suggested that these squeaking sounds may function in courtship behaviour and in defence (Robinson and Robinson, 1972).

Blest *et al.* (1963) demonstrated that the striated metepisterna in Arctiidae-Lithosiinae serve as tymbals. These organs can produce ultrasonic clicks when the moths are handled or are exposed to the ultrasonic sounds produced by bats (Dunning and Roeder, 1965). The moth sounds may serve an aposematic function, because those species that have the striated metepisternum are often distasteful to bats (Dunning, 1968).

In some Noctuidae ultrasonic clicking sounds are generated by momentary contact of the fore-wing apices at the top of the flight stroke during vigorous flight, and in *Heliothis* these sounds could be detected by individuals of the same species up to 100 cm away (Agee, 1971).

Although sound perception has been demonstrated in many moths, such as the Pyraloidea, Geometroidea and Noctuoidea, in which abdominal or thoracic tympanal organs are present, recent investigations have shown that some species that lack these organs are also able to detect sounds. For example, an ultrasonic perception has been demonstrated by Roeder (1972) in choerocampine Sphingidae. This is dependent on an enlarged second segment of the labial palp and a specialized distal lobe of the pilifer, both of which characterize this group of moths. In the normal position, the distal lobe of the pilifer, bearing a number of sensilla chaetica, is in contact with the scaleless inner surface of the palp. The bulbous palpal segment is almost entirely occupied by an air sac and its inner surface acts as acoustic interface, while the distal lobe of the pilifer is the site of the acoustic receptor. When a moth approaches or hovers before a blossom to feed, a high-pitched sound, such as the ultrasonic cry of a bat, results in the moth taking vigorous evasive action.

Bartholomew and Heinrich (1973) have added considerably to previous information on the body temperatures of moths in flight (p. 778). They found in several families of tropical moths that the thoracic and abdominal temperatures were consistently higher than ambient temperatures during flight, and that thoracic temperatures far exceeded abdominal temperatures. Thoracic temperatures were independent of ambient temperatures from 7° to 17° C, but increased with wing loading; except in the Arctiidae and Amatidae, they were independent of body weight. Normally, flight temperatures did not exceed 45° C. Even relatively small moths had a thoracic flight temperature of 15° to 17° C, and one 216 mg noctuid had a thoracic flight temperature of 36.9° C in an

air temperature of 7° C. Pre-flight wing vibration had been reported previously in Sphingidae and Saturniidae, and to these Bartholomew and Heinrich added Lasiocampidae, Arctiidae, and Amatidae. They did not observe this behaviour in Pyralidae and Geometridae.

Suborder ZEUGLOPTERA

Detailed studies of the morphology of the adult head and alimentary canal in the Micropterigidae and three of the families currently referred to the Dacnonypha led Kristensen (1968a, b, 1971) to list a series of advanced characters in which the Zeugloptera differ from the Trichoptera but resemble Dacnonypha. Some of these have already been noted on p. 785. Others include the presence of a medial process of the corpus tentorii, the presence of lateral bundles of setae on the labrum, the absence of a tentorial adductor of the mandible, the presence of a separate, slender cranio-stipital muscle, the relative length of the segments of the maxillary palp, the presence of an Eltringham's organ (a sensory receptor) on the postmentum, the absence of a dorsal muscle of the salivarium, the presence of a special apodeme at the upper end of the pterothoracic pleural costae, the absence of cerci in the female, the immediate separation of the labial nerve and the frontal ganglion connective, and the unpaired connectives between abdominal ganglia. Although the Zeugloptera share many primitive features with the Trichoptera and other panorpoid orders, these do not provide evidence for a closer phylogenetic relationship to them rather than to the Lepidoptera. Kristensen's work therefore supports the view that the Trichoptera probably diverged first from the stem leading to the Zeugloptera, Dacnonypha and the higher Lepidoptera. Certain features of larval morphology provide the only phylogenetic difficulties for regarding the Zeugloptera as a suborder of the Lepidoptera.

Suborder DACNONYPHA

As noted on p. 787, Kristensen (1967) has established the family Agathiphagidae

for the south-west Pacific genus *Agathiphaga*. Similarly Common (1973) has proposed a monotypic family Lophocoronidae for the 'undescribed genus' referred to on the same page. Eriocraniidae should therefore be deleted from the Australian list, and the two Australian families may be distinguished by the following couplet.

Galeae a pair of rounded lobes; maxillary palpi 5-segmented; tibial spurs 1-4-4

Agathiphagidae

Galeae modified to form short haustellum; maxillary palpi 4-segmented; tibial spurs 0-2-4

Lophocoronidae

As noted on p. 100, Mutuura (1972) concluded from his study of the female genital organs that the exotic families Neopseustidae and Mnesarchaeidae should be removed from the Dacnonypha. On other grounds Kristensen (1968b) had already suggested that these two families are the most advanced in the Dacnonypha and together form a monophyletic group within the sub-order. After studying the internal female genitalia of *Mnesarchaea*, Dugdale (1974) confirmed Mutuura's view, and thought that Neopseustidae and Mnesarchaeidae, together with the Hepialoidea, represent a primitive element of the Ditrysia.

Agathiphagidae (1 sp.; Figs 36.10A, 11B, 12D-F, 14C). Very small; head rough-haired; ocelli absent; antennae filiform; mandibles present, functional, dentate; maxilla with lacinia present; galea a prominent rounded lobe with concave inner face; maxillary palpi 5-segmented, folded; labial palpi 3-segmented, elongate subapical sensory invagination; epiphysis present, tibial spurs 1-4-4; fore wing with prominent jugum, humeral vein vestigial, Sc forked but Sc₁ vestigial, R₁ simple or apically bifid, vestigial cross-vein sometimes joining Sc₂ and R₁, R₂ and R₃ stalked, R₃ connected to R₄₊₅ by vestigial cross-vein, R₄ and R₅ stalked, R₄ to costa, R₅ to apex or termen, M vestigial in discal cell, M₃ sometimes bifid distally (or M₄ present), CuP present, a vestigial oblique cross-vein connecting CuA and CuP, 1A, 2A and 3A confluent distally, a vestigial cross-vein between 1A and 2A; hind-wing venation

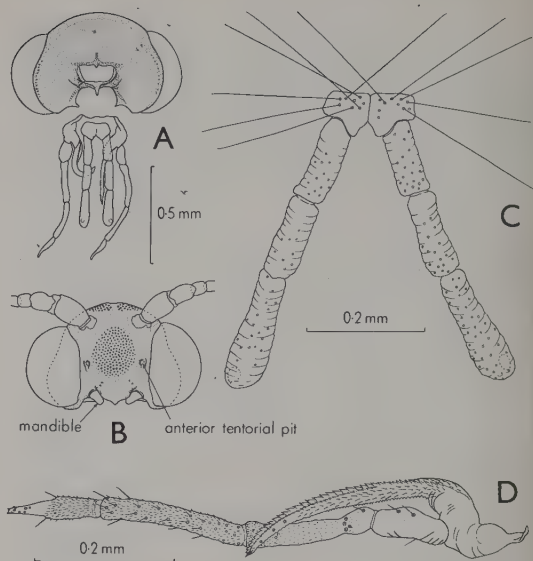


Fig. 36. *Lophocorona pediasia*, Lophocoronidae: A, B, head and mouth-parts, posterior and anterior; C, labial palpi; D, maxilla.

[I. F. B. Common]

as in fore wing, but 1A and 2A confluent distally; male with paired ventral processes protruding from abdominal segment 5; female with posterior segments of abdomen extensible, functioning as a probing ovipositor, posterior apophyses fused posteriorly, 2 pairs of anterior apophyses, a single genital opening on segment 9-10. Larva apodous, stout, head flexed beneath thorax, adfrontal sutures absent, stemmata reduced to a pair of pigmented spots, body cuticle densely spinulose, setae minute; within seeds of *Agathis*. Pupa with mandibles hypertrophied, asymmetrical, tarsi with paired claws; in an oval cell within seeds of *Agathis*.

Very few adults of *Agathiphaga queenslandensis* Dumbleton are known, although larvae occur commonly in the seeds of *Agathis robusta* in south-eastern Queensland, where they may cause a significant reduction in the viability of seed used for the establishment of kauri pine forests. Similar larvae also occur in the seeds of *A. palmerstoni* in northern Queensland. Pupation is delayed, sometimes for periods of some four years, by larval diapause in a hard resinous cell within

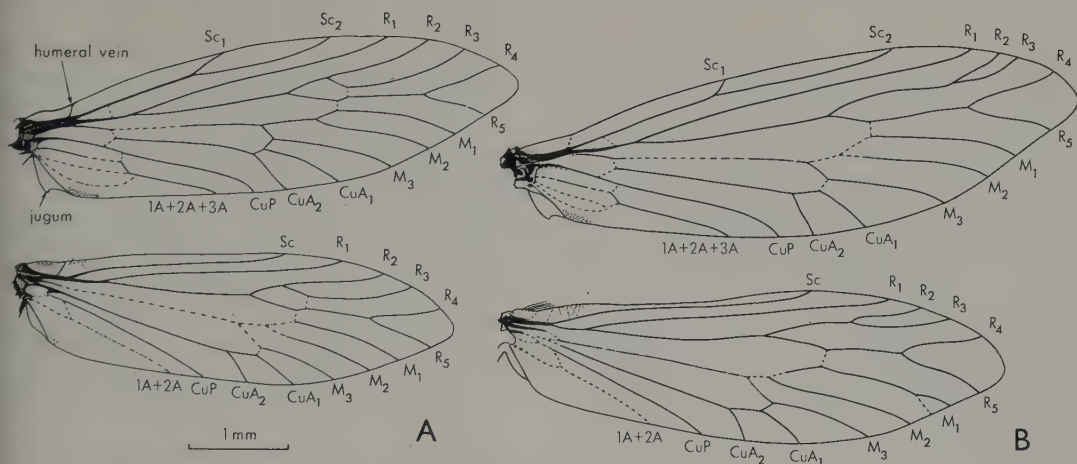


Fig. 37. Wing venation of Lophocoroninae: A, *Lophocorona pediasia*; B, *L. melanora*.

[I. F. B. Common]

the seed. Pupation occurs in this cell and the flimsy pupal cuticle is left protruding from the seed after ecdysis.

Lophocoroninae (3 spp.; Figs 36–8). Very small; head with long roughened hairs; ocelli absent; antennae filiform; mandibles present, non-functional; maxilla without lacinia; galeae modified to form a short probably functional haustellum; maxillary palpi long, 4-segmented, folded; labial palpi 3-segmented, with a small subapical sensory invagination; epiphysis absent, tibial spurs 0-2-4; fore wing with jugum small, humeral vein vestigial, Sc forked, R_1 simple, R_2 and R_3 stalked, R_3 sometimes connected to R_{4+5} by a vestigial cross-vein, R_4 and R_5 stalked, R_4 to costa and R_5 to termen, M present in discal cell, CuP present, 2A and 3A vestigial, distally confluent with 1A, a vestigial cross-vein present between CuP and 1A; hind wing with Sc and R_1 simple, CuP present, 1A and 2A vestigial, confluent distally; male with paired ventral processes on abdominal segment 5.

Only adult males of *Lophocorona* are known. *L. melanora* Common (Fig. 38B) was taken at the end of May in dry sclerophyll forest at Canberra. *L. astiptica* Common was collected near Coolgardie, Western Australia, and *L. pediasia* Common (Fig. 38A) in Western Australia and South Australia, in a narrow low-rainfall belt adjacent to the Great

Australian Bight. The early stages are unknown.

Suborder MONOTRYZIA

Mutuura (1972) suggested the transfer of the Adeloidea from the Monotryzia to the Dacnonypha primarily because of the similarity of their modes of oviposition to that of

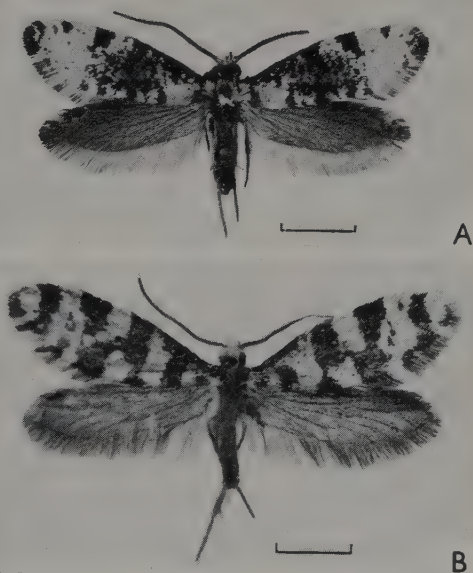


Fig. 38. Lophocoroninae: A, *Lophocorona pediasia*; B, *L. melanora*. Scales = 2 mm.

[Photos by J. P. Green, D. Wilson]

the Eriocraniidae. There appears to be no other support for this proposal.

Adelidae. The endemic incurvariine genus *Perthida* (2 spp.; Common, 1969b) includes the jarrah leaf miner *P. glyphopa* Common, a major pest of *Eucalyptus marginata* in south-western Australia (p. 115).

Suborder DITRYSIA

The phylogeny of the ditrysian superfamilies was examined by Brock (1971) using morphological data largely unstudied by previous authors. Special attention was given to the more advanced superfamilies. He selected five body regions of the adult which seemed to show progressive differences in character complexes of a kind likely to demonstrate superfamily evolution. These were: the radial venation of the fore wing; the sternopleural region of the mesothorax; the articulation of metathorax and abdominal sternum 2; the articulation of metathorax and abdominal tergum 1; the metathoracic furca or endosternite.

Brock removed the Choreutidae (formerly included in Glyphipterigidae) and the Sesiidae from the Yponomeutoidea, transferring them to a superfamily Sesiioidea. He considered that the Sesiioidea, Cossoidea and Castnioidea showed a high level of character correlation with the Tortricioidea, and that these three, together with the Zygaenoidea and the Pyraloidea, probably had a common origin in an ancestral form related to existing Tortricioidea. The Cossoidea, Castnioidea and Pyraloidea, in turn, may have provided independent origins for more advanced superfamilies, the Cossoidea for the Bombycoidea, the Castnioidea for the Papilionoidea, and the Pyraloidea for the Geometroidea and Noctuoidea.

Novel modifications in classification proposed by Brock would affect the superfamily limits that were adopted in the original chapter. In the Cossoidea he included not only the Cossidae and the Metarbelidae, but also Limacodidae and the exotic families Ratardidae, Dalceridae, Megalopygidae and Chrysopolomidae. On the basis of his characters, the Cyclotornidae, which he had

not examined, would also be included in the Cossoidea. He removed *Dudgeonea* from the Cossidae, and tentatively referred it and the Hyblaeidae to his Sesiioidea; the immature stages of *Dudgeonea* are not known, but those of *Hyblaea* lend little support for such an intimate association. He restricted the Zygaenoidea to the one family Zygaenidae, removing the Epipyropidae and Heterogynidae to the Tineoidea. The Pyraloidea, he considered, should include the Alucitidae and Pterophoridae; the association of the last two families was rejected by Chapman in 1896 on the basis of pupal structure. Finally, he merged the Hesperioidea with the Papilionoidea, the Calliduloidea with the Geometroidea, the Sphingoidea with the Bombycoidea, and the Notodontoidea with the Noctuoidea. The respective relationships of these pairs of superfamilies cannot be disputed, but the necessity for their merging seems doubtful.

Hessel (1969) made a comparative study of the imaginal dorsal vessel in most of the ditrysian superfamilies and, although he admitted the severe limitations of basing phylogeny on only a few morphological characters, suggested modifications to accepted views on the phylogenetic sequence. He reasoned that the Saturniidae and Limacodidae, with a similar arrangement of the thoracic aorta, show a clear relationship to one another and that this line probably led to the more advanced moths. The Megalopygidae and Zygaenidae, on the other hand, have a more primitive type of aortal arrangement, more akin to that of Sesiidae, *Atteva* in the Yponomeutidae and the Tineidae-Acrolophinae. Other Tineidae, Psychidae and Gelechiidae resemble the Castniidae and Tortricidae. Cossidae, he thought, were connected on the one hand with the Saturniidae and on the other to the Hesperidae and Papilionoidea. Two distinct aortal types were recognized in the Bombycoidea, the Bombycidae having a geometrid-type arrangement and the Lasiocampidae and Eupterotidae a noctuid-type arrangement. Hessel therefore suggested that bombycid-like ancestors gave rise to the

Geometroidea and Sphingoidea and that, at a later stage, lasiocampid- and eupterotid-like ancestors provided the origin for the Noctuoidea.

The ways in which Brock's and Hessel's views are at variance with one another and with the system adopted in the main volume show that much comparative morphological work is still needed on all stages of the Lepidoptera.

Lyonetiidae. It is now generally accepted that *Comodica*, *Erechthias* and related genera, in which the tip of the fore wing is bent abruptly upwards, should be referred to the Tineidae.

Yponomeutidae. The relationships of the genus *Imma* have for long been a matter of controversy. Meyrick assigned it to the Glyphipterigidae, Forbes in 1954 to the Yponomeutidae, and Gates Clarke in 1955 suggested that it may have been ancestral to the Noctuidae. On the basis of adult thoracic structures Brock (1971) included *Imma* in the family Choreutidae of his Sesiioidea.

The larvae of *I. acosma* Turn., recently discovered feeding openly on the foliage of *Hymenanchera dentata* in New South Wales, do not indicate a close relationship to *Choreutis*. The larva has 3 prespiracular (L) setae (see Fig. 36.9) on the prothorax, and the lateral (L) setae on the abdomen are not closely associated. The ventral prolegs are slender, the crochets of each arranged in a relatively straight median longitudinal band or uniordinal mesoserries of few crochets. Some secondary setae are present, especially in the subventral groups. Dorsal, subdorsal and lateral setae, as well as some setae on the head, have minute lateral spicular branches, and the two apical setae of the prothoracic legs are broadly spatulate. Pupation takes place beneath a flimsy silken network film spun across a depression. The maxillary palpi of the pupa are very reduced, the abdomen is without dorsal spines, and segments 3 to 5 are movable. The pupa is not protruded from the cocoon at ecdysis.

This combination of larval and pupal characters supports Brock's contention that the genus is misplaced in the Glyphipteri-

gidae, or even in the Yponomeutidae, but suggests a position well in advance of *Choreutis*. The naked haustellum and the presence of chaetosemata in the adult would make the genus anomalous in the Gelechioidea, and the ventral prolegs and the presence of 3 prespiracular setae on the prothorax of the larva would exclude it from the Copromorphoidea. Its true phylogenetic position remains obscure.

Epermeniidae. The Australian species have been revised by Gaedike (1968, 1972), who recognized 18 species distributed between 3 genera, *Ochromolopis* (12 spp., including *eurybias* (Meyr.)), *Paraepermenia* (1 sp.) and *Epermenia* (5 spp.).

GELECHIOIDEA. Although the larvae of most families of Gelechioidea have abdominal setae L1 and L2 approximated (p. 815), Agonoxenidae and Cynodiidae are exceptional in having these setae widely separated.

Physoptilidae (Fig. 39). As noted on p. 782, an undescribed species of *Physoptila* is known from Cape York, and a further 2 are now known from central Queensland and the Northern Territory. The somewhat trapezoidal hind wing, a subradial retinaculum in the female, and the male genitalia indicate a close relationship to the Gelechiidae. Despite the presence of CuP in both wings, Sattler (1973) has included the genus in the Gelechiidae. The early stages of the Australian species are unknown. One of 2 exotic species was reared in Java from larvae boring in the shoots of *Planchonia*

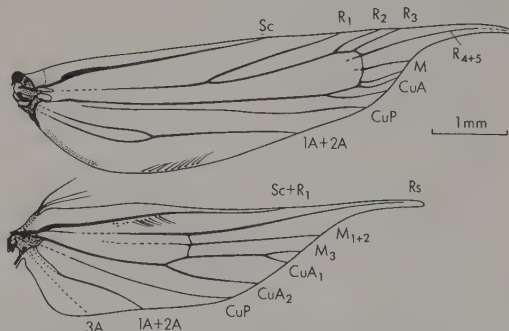


Fig. 39. *Physoptila* sp., Physoptilidae, wing venation. [B. Rankin]

(Myrtaceae), a genus of plants ranging from tropical Asia to northern Australia.

Castniidae. The early stages of the Australian genus *Synemon* have been very imperfectly known until recently, although larvae and empty pupal shells of *S. sophia* (White) were found to be associated with the sedge *Lepidosperma* by Tindale in 1928. The immature stages of *S. magnifica* Strand (Fig. 40) have recently been discovered near Sydney, where the larvae also feed on *Lepidosperma*. The eggs are elliptical, with four very prominent longitudinal ridges and numerous fine transverse striae. Early-instar larvae have 2 transverse bands of uniordinal crochets on the ventral prolegs, whereas the mature larvae lack crochets altogether. In general appearance the whitish or pinkish larvae resemble those of Cossidae, with stout thorax and abdominal segments tapering posteriorly. They also have a few secondary setae in later instars. They at first tunnel in the butt of the *Lepidosperma* tussock and later feed externally on the butt of the plant below ground level. Pupation occurs in a vertical tubular shelter constructed of silk and plant debris, projecting above the surface of the soil near the base of the plant.

Anthelidae. *Munychryia* (2 spp.) and *Gephyroneura* (1 sp.) were separated from

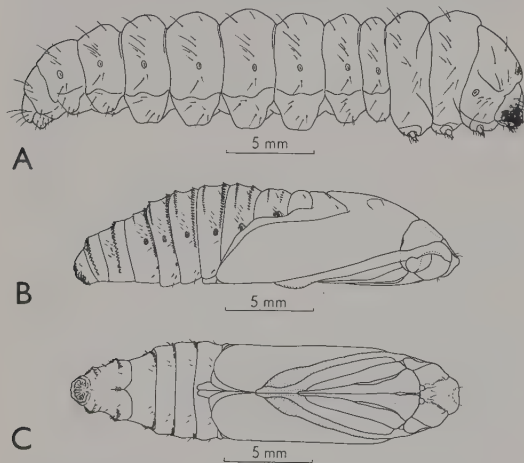


Fig. 40. *Synemon magnifica*, Castniidae: A, larva; B, C, pupa, lateral and ventral.

[I. F. B. Common]

the remaining Anthelidae by Common and McFarland (1970) as the subfamily Munychryiinae. A haustellum is retained in these genera, and the oblique sclerotized ridge between R_2 and R_3 of the fore wing of most Anthelinae is here extended to R_1 . In distinguishing the subfamily, special emphasis was given to the larva of *Munychryia* which lacks the long dense secondary setae arranged on verrucae that are found in all known species of Anthelinae. In *Munychryia* the secondary setae, which are restricted to the anal prolegs of the first instar and are scattered over the whole body in later instars, are extremely short and spatulate and not grouped on verrucae. *Munychryia* larvae have a longitudinal striped pattern which effectively conceals them as they lie along the branchlets of *Casuarina* upon which they feed.

Sphingidae. In a revision of the North American Sphingidae, Hodges (1971) divided the family into only two subfamilies, Sphinginae and Macroglossinae. In separating the suprageneric groups, he placed considerable reliance on characters provided by the genitalia in both sexes. Rothschild and Jordan's subfamilies Acherontiinae and Ambulicinae were included in the Sphinginae, and their other 3 subfamilies Sesiinae, Philampelinae and Choerocampinae in the Macroglossinae. Rothschild and Jordan, on the other hand, thought that the Choerocampinae were a sharply circumscribed group, distinguished from all other Sphingidae by the peculiar structure of the second segment of the labial palpi and of the pilifers. Roeder and Treat (1970) have concluded that these structures form an ultrasonic receptor, and agree that they are unique to this group of hawk moths, although the possibility of sound perception by means of other organs is not excluded in other Sphingidae that are exposed to bat predation.

Notodontidae. The Indo-Australian Notodontinae and Thaumetopoeinae were treated as separate families by Kiriakoff (1968, 1970). He referred 53 Australian Notodontinae to 28 genera, many of which also occur in New Guinea or south-eastern Asia.

He transferred *capucina* Feld., one of the two species previously assigned to *Neola*, to *Hylaeora*; the larvae, which feed on *Eucalyptus*, support this. He referred 40 Australian species of Thaumetopoeinae to 14 largely endemic genera. *Discophlebia*, formerly referred to the Notodontinae, was stated to be related to *Oenosanda*. The larvae of *D. catocalina* Feld. have much in common with those of *O. boisduvalii*, but differ in having the uniordinal crochets normal for the family, whereas in *Oenosanda* they are biordinal. The large genus *Epicoma* was divided into 3 genera, *Epicomana* (1 sp.),

Marane (8 spp.) and *Epicoma* (7 spp.).

As long ago as 1887 E. B. Poulton observed that the larvae of *Cerura* use the bifid eversible organ beneath the head to spray formic acid over a potential enemy if attacked. Eisner *et al.* (1972) have shown that, in addition to formic acid, the secretion of the North American notodontid *Heterocampa* contains two ketones, undecanone and tridecanone. The secretion caused intense irritation to spiders and ants; but, as ants themselves secrete formic acid, its effect on them must depend on the other components.

37

HYMENOPTERA

(Wasps, bees, ants)

by E. F. RIEK and JOSEPHINE C. CARDALE

Anatomy

O. Richards (1971) studied thoracic spiracles and associated structures in Hymenoptera, and van der Vecht (1968) the terminal gastral sternite in female Vespidae, both finding significant characters for use in classification. The female reproductive system was studied by Robertson (1968), who related changes in morphology to the development of the venom apparatus, and by Copland and King in a series of papers on Chalcidoidea (e.g. on Torymidae, 1973). H. Evans (1969b), studying phoretic copulation, found striking differences in the modifications of male and female genitalia in Bethyloidea and Thynninae, which confirmed the belief that phoretic copulation has evolved several times independently.

Suborder SYMPHYTA

Guiglia (1973) listed 10 species of Australian **Orussidae**, and stressed Antarctic distribution in the family. Riek (1970b) redefined **Pergidae**-Phylacteophaginae, mainly on the basis of wing venation, and described a second genus, *Leptoperga* (1 sp.). Food plants of Pergidae-Euryinae are still unknown, apart from the record by K. Moore (1957) of *Polyclonus atratus* larvae skeletonizing dead leaves of *Eucalyptus* and *Angophora*.

Suborder APOCRITA

MEGALYROIDEA. Taylor (1967) discussed the biology of *Schlettererius cinctipes* (**Stephanidae**), introduced from California against *Sirex noctilio* and later released in Tasmania.

ICHNEUMONOIDEA. Since Townes *et al.* (1961) catalogued the Indo-Australian **Ichneumonidae**, Townes (1969–71) has revised many of the genera of the world. Subfamily and tribal divisions in **Braconidae** are still not generally agreed upon; Čapek (1970) gave a classification based on larval cephalic structures and biological data. Mackauer (1968) catalogued the Aphidiinae, and Shenefelt (1969–73) is cataloguing species in other subfamilies. Fischer (1966) revised Indo-Australian Opiinae. Blackith (1967a) described *Perilitus morabinarum* (Euphorinae), the first known hymenopterous primary parasite of post-egg stages of Acridoidea.

PROCTOTRUPOIDEA. The **Loboscelidiidae** (p. 910) were originally placed in the Bethyloidea. Kozlov (1970) divided the **Proctotrupidae** into Mesoserphinae (1 fossil genus) and Proctotrupinae (16 genera in 5 tribes), placing *Austroserphus* and *Acanthoserphus* in the tribe Austroserphini. **Platygastridae** are divided into 3 subfamilies, Sceliotrachelinae being represented in Australia by *Platygastroides*. Hickman (1968) described **Scelionidae** bred from spider eggs, and Masner (1969) listed previously known trans-Antarctic relationships in the Proctotrupoidea when defining *Austropria* (**Diapriidae**), closely related to genera in South America.

CYNIPOIDEA. Riek (1971b) transferred Eucoilinae and Charipinae to **Figitidae** when he erected a new subfamily **Cynipidae**-Austrocynipinae for *Austrocynips mirabilis* from seeds of *Araucaria cunninghamii*.

CHALCIDOIDEA. Ramírez (1969), investigating the mechanism of pollen transfer by female **Agaonidae**, found corbiculae on the fore coxae and mesosterna of many species. *Blastophaga psenes*, unlike other species of the genus, lacks both pairs; *Pleistodontes imperialis* has sternal corbiculae only. Hill (1967) catalogued the world genera of fig wasps, listing from Australia 3 genera of Agaonidae and 9 of **Torymidae**, 6 in the Sycophaginae and 3 in the new sub-

family Epichrysomallinae. Doutt and Viggiani (1968) listed over 30 genera and 170 species of **Trichogrammatidae** from Australia, with *Oligosita* (37 spp.) the largest genus. Dahms (1973) described the courtship behaviour of *Melittobia australica* (**Eulophidae**-Tetrastichinae), a dimorphic species whose male has abbreviated wings and modified antennae. Burks (1971) divided the **Eurytomidae** into 8 subfamilies, with 8 genera from Australia placed in Eurytominae, Harmolitinae and Eudecatominae, and an additional 7 genera unplaced. *Desantisca* (Eurytominae), parasitic in the egg sacs of the red-back spider *Latrodectus hassellti*, has been recorded from the Australian region.

POMPILOIDEA. The classification of Australian **Pompilidae** is in an unsatisfactory state, with few of the old species having been re-examined for modern placement and a large number of new ones awaiting description. Work by H. Evans (1971, 1972a–c) gives some idea of the size of the problem in the number of new genera and species he has recorded from Australia. *Iridomimus* (Pepsinae-Cryptocheilini) was erected for two striking ant mimics (Fig. 37.28B). *Cteniziphontes* (Pepsinae-Ctenoceratini) is unique in Pompilidae (and almost unique in Aculeata) in having 13 antennal segments in the female (referred to as *Chirodamus* sp. on p. 931). Ctenoceratini, specialist predators of trap-door spiders (Ctenizidae), were previously known from South America and Africa with one genus extending into India and Java. Evans and Matthews (1973a) studied the biology of 12 species of Pepsinae and Pompilinae.

SCOLIOIDEA. Ridsdill Smith (1970) studied the biology of *Hemithynnus hyalinatus* and compared it with other species.

VESPOIDEA. O. Richards (1968) described 3 new species of **Masaridae** and gave additional records of other species. Richards (personal communication) is currently preparing a revision of Australian **Vespidae** (*Polistes* 8 spp., *Ropalidia* 24 spp., *Vespula* 2 introduced spp.). Soika (1969)

revised Australian **Eumenidae**-Discoeliinae (=Zethinae), including 23 species and 7 subspecies in 6 genera.

SPHECOIDEA. Evans and Matthews (1973b) studied Australian *Bembix* (**Sphecidae**-Nyssoninae-Bembicini, 80 spp.) and gave detailed information on their biology. The usual prey are Diptera, but some species utilize Odonata and Hymenoptera. Leclercq (1972) revised Asian and Pacific species of *Dasyproctus* (Crabroninae; 6 Australian spp.), and Tsuneki (1968) revised Australian *Cerceris* (Cercerinae; 36 spp.). Evans and Matthews (1970, 1971a, b) studied the biology of Australian *Cerceris*, Crabronini and Nyssoninae, and found them to have generally similar habits to their relatives in the northern hemisphere. On the basis of nest-building behaviour and larval morphology, *Austrogorytes* (Gorytini) is a very generalized nyssonine. Prey found in

nests of *A. bellicosus* belonged exclusively to the endemic family Eurymelidae, but *A. perkinsi* has been captured carrying a small cicada. Matthews and Evans (1971) studied the biology of two species of *Sericophorus* (Larrinae-Miscophini) and found distinct differences in behaviour and prey.

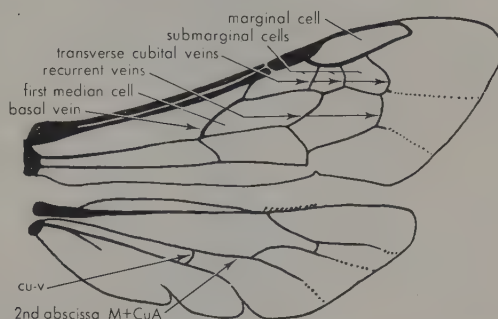


Fig. 41. Wing of an anthophorid bee, showing veins and cells referred to in the key.

Superfamily APOIDEA

by CHARLES D. MICHENER

Because the key to the families on pp. 945-6 uses characters that are often difficult to see,

an artificial key based on more obvious characters is provided here.

1. With one or two submarginal cells (Fig. 41) 2
With three submarginal cells 8
- 2(1). Marginal cell open at apex (distal wing venation much reduced); hind tibia of worker with corbicula (smooth area surrounded by long hairs) on outer side *Trigona* (**Apidae**)
Marginal cell closed at apex; corbicula absent 3
- 3(2). Stigma almost absent and basal to middle of wing (very large bees) *Xylocopa* (**Anthophoridae**)
Stigma distinct, distal to middle of wing 4
- 4(3). Inner hind tibial spur of ♀ greatly broadened basally so that whole spur is crescentic (north Queensland) **Melittidae**
Inner hind tibial spur not broadened basally 5
- 5(4). Arolia absent or essentially so **Megachilidae**
Arolia present and conspicuous between claws 6
- 6(5). Stigma very short, one-third as long as costal margin of marginal cell or less (tropical)
..... *Anthidiellum* (**Megachilidae**)
Stigma more than half as long as costal margin of marginal cell 7

- 7(6). Mesepisternum without any evidence of pre-episternal groove below scrobal suture (Fig. 37.5B); scopa of ♀ (p. 874) on tibia and basitarsus; proboscis long *Braunsapis*, *Exoneura*, *Inquilina* (**Anthophoridae**)
 Mesepisternum with distinct pre-episternal groove below scrobal suture; scopa of ♀ on femur (and elsewhere) or absent; proboscis shorter, apices of galeae in repose not reaching posterior end of proboscival fossa **Colletidae**
- 8(1). Hind tibial spurs absent; hind tibia of worker with corbicula on outer side *Apis* (**Apidae**)
 Hind tibial spurs present; hind tibia without corbicula 9
- 9(8). Marginal cell much shorter than first median; vein cu-v of hind wing strongly oblique and much more than half as long as second abscissa of M+CuA (except in *Nomada*) **Anthophoridae**
 Marginal cell little if any shorter than first median; vein cu-v of hind wing transverse and usually less than half as long as second abscissa of M+CuA (see *Stenotritinae* in *Colletidae*, in which cu-v is elongate and oblique in a different way) 10
- 10(9). Stigma almost absent (large, robust bees) **Anthophoridae-Xylocopini**
 Stigma distinct, longer than broad 11
- 11(10). Mesepisternum without pre-episternal groove or this groove only weakly suggested above scrobal suture; scopa of ♀ on tibia and basitarsus only; proboscis long, apices of galeae in repose reaching beyond posterior end of proboscival fossa *Ceratina* (**Anthophoridae**)
 Mesepisternum with distinct pre-episternal groove usually continuing below scrobal suture; scopa of ♀ on femur and elsewhere (rarely absent); proboscis shorter, apices of galeae in repose not reaching posterior end of proboscival fossa 12
- 12(11). First flagellar segment of antenna longer than scape **Colletidae-Stenotritinae**
 First flagellar segment shorter than scape 13
- 13(12). Third submarginal cell at least three-fourths as long as first and more than twice as long as second; pre-episternal groove extending but little below scrobal suture **Halictidae-Nomiinae**
 Third submarginal cell usually less than three-fourths the length of first and always less than twice as long as second; pre-episternal groove extending well below scrobal suture (except in *Hesperocolletes*, *Colletidae*) 14
- 14(13). Body with yellow integumental markings, including metasomal fasciae (minute species with pale wings) *Nomioides* (**Halictidae**)
 Without yellow integumental markings except sometimes on face (usually clypeus only) of ♂♂ 15
- 15(14). Basal vein of fore wing strongly curved (Fig. 37.36B); second recurrent and third transverse cubital veins usually distinctly weaker than first recurrent and first transverse cubital; prepygidial fimbria of ♀ divided medially by longitudinal median furrow or line with distinctive hair pattern (prepygidial fimbria absent in *Sphecodes*) **Halictidae-Halictinae**
 Basal vein of fore wing straight or gently curved; second recurrent and third transverse cubital veins as strong as other nearby veins; prepygidial fimbria of ♀ undivided **Colletidae-Colletinae**

Exley (1968–72) has revised several genera of *Colletidae-Euryglossinae*, and Houston (1969) has described the nests of several species. Houston (1970) also described a communal nest of *Lasioglossum* (*Chilalictus*) (*Halictidae-Halictinae*) in which

males were polymorphic (Fig. 42). He speculated that the large-headed, small-winged males function as soldiers, and if this is correct, it is the first record of male polymorphism in social Hymenoptera (Wilson, 1971). Houston (1971) described the nests of

Lithurge atratiformis (Megachilidae-Lithurginae) in unlined tunnels in dead wood, and Rozen (1973) found that the larvae are very

similar to those of Megachilinae. The larvae and pupae of *Amegilla* and *Thyreus* (Anthophorinae) were described by Cardale (1968).

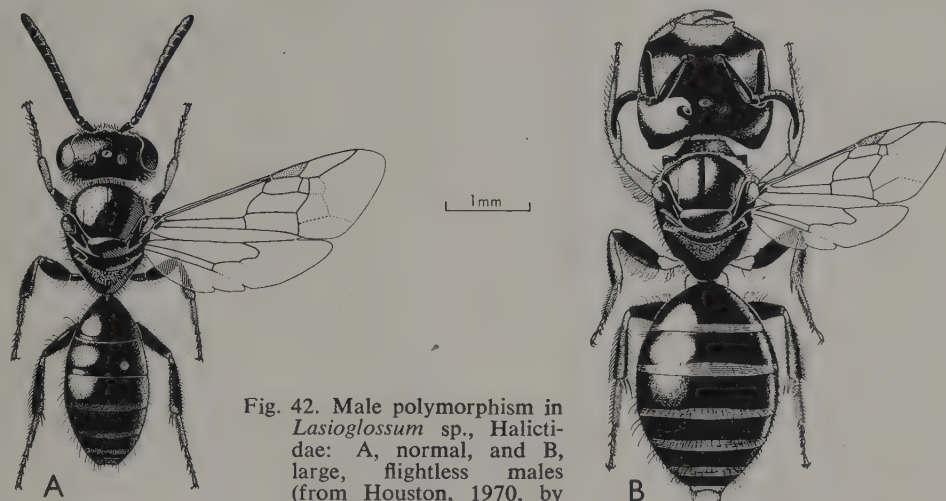


Fig. 42. Male polymorphism in *Lasioglossum* sp., Halictidae: A, normal, and B, large, flightless males (from Houston, 1970, by permission of the publishers).

Superfamily FORMICOIDEA

by R. W. TAYLOR

Broad aspects of the social biology of ants were reviewed by Wilson (1971), who discussed many Australian species. A useful synonymic list of world ant genera, with a table of their regional distribution, was presented by Brown (1973b). The bulldog ants (*Myrmecia*) have been subject to behavioural and ecological studies by Gray (1971), Robertson (1971) and Haskins *et al.* (1973), while Greenslade (1970) and Greaves (1971) have discussed the distribution and biology of the enigmatic 'races' of the meat ant *Iridomyrmex purpureus*. Techniques used for pheromone bioassay of ants were reviewed by Robertson and Orton (1971).

Taxonomic contributions include those of Brown on *Strumigenys* (1971a, 1973a) and *Pheidole vigilans* (1971b). The latter, like many early-described and widespread Aus-

tralian species, has accumulated an extensive synonymy based on type specimens scattered overseas. Various myrmecine genera have been reviewed by Taylor (1970, 1973). Recent Australian developments in the application of scanning electron microscopy in ant taxonomy (Taylor and Beaton, 1970; Taylor, 1973) could well revolutionize descriptive taxonomy of these insects, of which it is estimated that less than 50 per cent are currently named. The continuing larval studies of Wheeler and Wheeler (1971) have covered a number of Australian *Myrmecia* and *Bothroponera* species. Ants featured strongly in Taylor's review (in Walker, 1972, pp. 213-30) of insect biogeography in relation to climatic zones and plant associations in New Guinea and northern Cape York Peninsula.

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CORRIGENDA FOR MAIN VOLUME

Changes in the names of taxa since the book went to press are indicated by an asterisk (*). Minor errors that do not affect the sense have been ignored, but all known errors in the names of taxa have been corrected. The page number is at the left of the column and 'Plate' is abbreviated 'Pl.'

- 41 col. 1, lines 4–5: for '*para-oesophagael*' read '*para-oesophageal*', for '*sub-oesophagael*' read '*sub-oesophageal*', for '*commis-sures*' read '*connectives*'
- 61 col. 1, line 23: for 'mole' read 'molecule'
- 92 Fig. 4.9: for 'tettigoniid' read 'gryllacridid'
- 106 col. 2, lines 35–6: insert 'and' after 'Phyl-locnistidae'; delete 'and Lithocolletidae'
- 121 col. 2, line 11: *for '*exigua*' read '*irritans exigua*'
- 125 col. 2, line 3: for '*Strumeta*' read '*Dacus (Strumeta)*'
- 134 Fig. 5.40: for '*tasmaniensis*' read '*humilis*'
- 178 col. 2, lines 28–9: *for 'Clatrotitanidae' read 'Mesotitanidae'
- Pl.5 L: for '*violacea*' read '*viola*'
- Pl.6 U: *for '*Cerioides*' read '*Ceriana*'; V, *for '*Phanagenia*' read '*Fabriogenia*'; X, for '*Miscothyris*' read '*Clitemnestra*'
- Pl.8 G: *for '*chrysippe* (F.)' read '*cydippe* (L.)'
- 238 Fig. 12.8B: for '*Atalonella*' read '*Choro-terpes*'
- 277 col. 1, line 12: for 'ergum' read 'tergum'
- 282 col. 2, last line: for 'Aphididae' read 'Termitaphididae'
- 306 Fig. 19.1, and elsewhere: *for '*Labidura riparia truncata*' read '*Labidura truncata*'
- 317 in key and elsewhere: *for 'Nemouridae' read 'Notonemouridae'
- 331 in heading for Suborder: for 'ENISFERA' read 'ENSIFERA'
- 336 Fig. 21.5B: for '*pellucida*' read 'sp.'
- 341 col. 2, line 16: delete 'spiny'; line 30, for '2' read '3'
- 342 Fig. 21.10A: for '*crenaticeps*' read '*similis*'; C, for 'sp.' read '*pedestris*'
- 345 col. 2, line 21: after 'wing' insert 'when present'
- 358 Fig. 22.7: for '*Didymura*' read '*Didymuria*'
- 368–71 Figs 24.1, 24.4–6: *for '*Myopsocus griseipennis*' read '*Phlotodes australis*'
- 372 col. 1, lines 1–2: *for '*Sphaeropsocus*' read '*Sphaeropsocopsis*'
- 379 col. 1, line 38: *for '*australis*' read '*afri-cana*'
- 381 col. 2, line 27: *for 'Boopiidae' read 'Boopidae'
- 382 col. 2, line 6: for '*mellori*' read '*tasmanicus*'
- 382–3 *passim*: *for 'Boopiidae' read 'Boopidae'
- 389 Fig. 26.3A: transpose 'proepimeron' with 'proepisternum' and 'mesepimeron' with 'mesepisternum'
- 402 col. 1, lines 11–12: *for '*H. wilsoni* Evans' read '*Hemiowoodwardia wilsoni* (Evans)' and for '*Hackeria*' read '*Hackeriella*'
- 414 col. 1, line 12: for '4' read '5'
- 415 Fig. 26.33C: *for '*Neodartus*' read '*Neovulturmus*'
- 417 col. 1, line 7: *for '*Austroasca*' read '*Empoasca*'
- 419 Fig. 26.36G, H: transpose '*Creiis costatus*' with '*Creiis periculosa*'
- 424 col. 1, line 24: for '*Nothophagus*' read '*Nothofagus*'
- 437 Fig. 26.47A: for '*modestum*' read '*dilutum*'
- 441 Fig. 26.51C: *for '*Omania*' read '*Corallo-coris*'; col. 2, line 1: insert 'and *Corallo-coris*' after '*Omania*'; line 7, for 'O.' read 'C.'
- 443 Fig. 26.55B: *for '*bidentatus*' read '*australis*'
- col. 2, line 1: *for '*bidentatus* Montr.' read '*australis* (F.)'
- 452 col. 1, line 14: *replace by 'genus here is *Poecilometis*'
- 454 col. 2, line 2: for '*australica*' read '*australicus*'
- Fig. 26.71A: for '*Ochterus marginatus*' read '*Megochterus nasutus*'
- 455 col. 1 below key, line 14: for '4' read '3'
- 456 Fig. 26.72C: for '*congrex*' read '*australicus*'

- 457 col. 2, line 6: for '5' read '7'; lines 9–10, delete 'and the allied genus *Corixanecta* in New Zealand,' and for 'are' read 'is'
- 461 col. 1, line 43: transpose 'males' and 'females'
- 463 col. 1, line 31: *for '*brevicornis* (Bagn.)' read '*frici* (Uzel)'
col. 2, line 5: *for '*striatus* Osb.' read '*obscurus* (Muller)'
col. 2, beneath 'TUBULIFERA', line 1: *for '*Phlaeothrips*' read '*Hoplothrips*'
- 464 col. 1, line 2: *for '*Phlaeothrips*' read '*Hoplothrips*'
col. 1, line 10: delete 'Both *Froggattothrips* and'; line 11, *replace by '*Rhopalothripoides* contains a minute species'; line 14, *for '*dimidiatus* (Hood)' read '*propinquus* (Bagn.)'
- 468 Fig. 28.4C: for 'abdominal gill' read 'abdominal process'
- 470 col. 2, lines 6–7: for '*Protochauliodes*' read '*Austrochauliodes*' and replace 'occurs . . . America' by 'is endemic'
- 471 col. 1, line 3: for '*Protochauliodes*' read '*Austrochauliodes*'
- 473 Fig. 29.1: for '*Chrysopa*' read '*Dictyo-chrysa*'
- 481 col. 2, lines 28–9: for '*Odeosmylus*' read '*Oedosmylus*'; line 31, for '*Perisemidalis*' read '*Neosemidalis*'
- 484 col. 2, line 4: for '*Parasemidalis*' read '*Neosemidalis*'
- 503 Fig. 30.6C: for '*Omma*' read '*Cupes*'
- 512 col. 1, last line: for '*Rhizopertha*' read '*Rhyzopertha*'
- 517 under 'CLASSIFICATION', col. 2: *for '*Eurypogonidae*' read '*Artemotopidae*'; below 'Elateroidea' insert 'Cebrionidae (250, 0)'; *for '*Trixagidae*' read '*Throsco-dae*'; col. 3, *for '*Sarothriidae*' read '*Jacobsoniidae*'
- 518 in classification, col. 2: *for '*Elacatidae*' read '*Othniidae*'; col. 3, *for '*Proterrhini-dae*' read '*Aglycyderidae*'
- 524 col. 1, line 9: insert '(ANISOCHAETA)' before '2'
- 531 col. 1, line 4: for 'Wehnke' read 'Wehncke'
col. 2, line 6: for '*Homeodytes*' read '*Homoeodytes*'
- 540 in couplet 5 (twice): for 'trochanters' read 'trochantins'
- 542 col. 2, line 27: for 'trochanters' read 'trochantins'
- 545 col. 1, last line: for '*Termitaptocinus*' read '*Termitoptocinus*'
- 557 col. 1, line 12: for '*Cryptotermes*' read '*Coptotermes*'
- 564 col. 1, line 6: for '8' read '7'
- 572 col. 1, line 16: for '*cinctus* Redtenb.' read '*bellulus* Guérin'
col. 2, line 26: for 'labume' read 'labrum'; line 28, for 'cotxa' read 'coxa'
- 576 Fig. 30.63: *for '*Bostrychoplites*' read '*Mesoxylion*'
col. 2, line 32: for '*Rhizopertha*' read '*Rhyzopertha*'
- 577 col. 2, line 13: delete 'Both' and insert 'The', delete 'and adults'; line 17, for 'un-seasoned' read 'seasoned'
- 586 col. 1, last line: delete '*Tristaria*' (belongs to Lyctidae)
- 598 col. 1, line 48: for '*Amarygminus*' read '*Amarygmus*'
- 613 col. 1, line 35: for '3' read '4'
- 617–20: *for terminations of curculionid sub-family names '-rrhynchinae' and '-rrhini-nae' read '-rhynchinae' and '-rhininae', *and for terminations of generic names '-rrhynchus' and '-rrhinus' read '-rhynchus' and '-rhinus'
- 618 couplet 6: *for 'BALANINAE' read 'CURCULIONINAE'; couplet 9, *for 'MOLYTINAE' read 'PHRYNIXINAE'; couplet 18, *for 'TRACHODINAE' read 'ACICNEMINAE'; couplet 23, *for 'SIPALINAE' read 'RHYNCHOPHORINAE-Sipalini'
- 619 col. 2, line 11: *for 'MOLYTINAE' read 'PHRYNIXINAE'
- 620 col. 1, line 1: *for 'CURCULIONINAE (Hylobiinae)' read 'PISSODINAE'; line 9, after '*cylindrirostris* F.' insert '(HYLOBIINAE)'
- 628 col. 2, line 5: for '*Bembicinus*' read '*Bembecinus*'
- 630 col. 1, line 40: for '*australiensis*' read '*australensis*'
- 634 col. 1, line 6: for '*Bembicinus*' read '*Bembecinus*'
- 635 col. 1, line 4: for '*australiensis*' read '*australensis*'
- 660 Fig. 34.3D: *for '*exigua*' read '*irritans exigua*'
- 672 Fig. 34.11: C and D, for 'respiratory horn' read 'prothoracic spiracle of pupa'; E, the anterior end is at bottom
- 685 col. 1, line 31: *for '*Semnotes*' read '*Leptotarsus*'
- 686 Fig. 34.15A: for '♂' read '♀'; F, *for '*Semnotes*' read '*Leptotarsus*'
- 692 Fig. 34.17G: for '*M₁₊₂*' read '*M₁*'

- 695 col. 2, line 39: for '*Colbostema*' read '*Colobostema*'
- 703 col. 1, last line: *for '*Altermetoponia*' read '*Inopus*'
- 708 Fig. 34.24, scale: for '20' read '10'
- 712 col. 1, line 20: for ' M_4 ' read ' M_{3+4} '
- 713 Fig. 34.26A: for ' M_3 ' read ' $M_{3+4} + CuA + 1A$ ' and delete ' $M_4 + CuA$ '
- 714 col. 2, line 9: *for '*Ceriodes*' read '*Ceriana*'
- 717 couplet 39, line 2: after 'sheath' add 'except in Pseudopomyzidae'
- 720 Fig. 34.28F: *for '*Adapsilia*' read '*Cardiacera*' and insert '♀' before 'abdomen'
- 722 col. 2, line 12: for '*Trepidarioides*' read '*Cothornobata*' and *for '*Gongylocephala*' read '*Crepidochetus*'
- 723 Fig. 34.29A: for '*tenuipes*' read '*terminalis*'
- 726 col. 1, line 2: for '*Oecothea*' read '*Aecothea*'
- col. 2, line 12: for 'Otitoidea' read 'Tephritoidea'
- 727 Fig. 34.31A: *for '*scutellata*' read '*antipodum*'
- col. 2, line 2: for '*Anguillulina* (*Fergusobia*)' read '*Fergusobia*'
- 732 col. 1, line 11: for '*flavus*' read '*flava*'
- col. 2, line 27: for 'STOMOXINAE' read 'STOMOXYINAE'
- 734 col. 1, line 30: for 'STOMOXINAE' read 'STOMOXYINAE'
- col. 1, line 37: *for '*exigua*' read '*irritans exigua*'
- 743 col. 2, line 10: for 'Oestropsinae' read 'Macronematinae'
- 749 col. 1, last line: for 'Oestropsinae' read 'Macronematinae'
- 754 col. 2, line 20: for '*Agapetus*' read '*Synagapetus*'
- 761 col. 2, lines 34, 42: '*Ausmanthrus*' is a *nomen nudum*
- 769 col. 2, line 23: for 'subcubital' read 'subcostal'
- Fig. 36.4D: for '*Urisephita*' read '*Uresiphita*'
- 770 col. 1, line 25: after '1-7' insert 'occasionally on 8 in females, e.g. some Hepialidae'
- 777 Fig. 36.10D: for more posterior 'genital scar' read 'anal scar'
- 781 col. 1, line 25: *for '*Ochrogaster*' read '*Teara*'
- col. 2, line 43: *for '*Ochrogaster*' read '*Teara*'
- 782 under 'CLASSIFICATION' and wherever occurring elsewhere: for 'DACHNONY-PHA' read 'DACNONYPHA', for 'Incurvarioidea' read 'Adeloidea', for 'Incurvariidae' read 'Adelidae', for 'Aegeriidae' read 'Sesiidae', for 'Elachistidae' read 'Cynodiidae', for 'Scythridae' read 'Scythruidae', for 'Stathmopodidae' read 'Tinaegeriidae', for 'Stenomidae' read 'Stenomatiidae'
- 789 col. 2, line 23: for '2-6' read '2-7 in male, 2-6 in female'
- 798 Fig. 36.17D: *for '*Clysiana*' read '*Eupoe-cilia*'
- 799 Fig. 36.18G: *for '*Olethreutes melano-cycla*' read '*Lasiognatha mormopa*'
- 801 col. 1, line 6: *for '*Olethreutes melano-cycla* (Turn.)' read '*Lasiognatha mormopa* (Meyr.)'
- 802 col. 1, line 3: *for '*Clysiana*' read '*Eupoe-cilia*'; line 5, for 'C.' read 'E.'
- col. 2, line 11: for '4-7, 4-8, or 5-8' read '2-7, 3-7, or 4-7'
- 807 col. 1, line 7: for 'have ocelli and' read 'lack ocelli but have'
- 809 col. 1, line 3: for '5-8' read '4-7'; line 4, for '5-7' read '4-6'
- 813 col. 2, line 36: for '*Ogmograptus*' read '*Ogmograptis*'
- 816 col. 2, line 7: *for '*alcyonipenella* Koll.' read '*frischella* (L.)'
- 819 col. 1, line 17: for '*Vanacela*' read '*Vanicela*'
- 820 col. 1, penultimate line: for '*Hoffmannophila*' read '*Hofmannophila*'; last line, for '(Steph.)' read '(L.)'
- 825 col. 2, lines 4, 17: for '*Brachiacma*' read '*Brachyacma*'; line 19, for 'Leguminosae' read 'Mimosaceae'
- 834 Fig. 36.38F: for '*Urisephita*' read '*Uresiphita*'
- 836 col. 2, line 38: *for '*Psara*' read '*Herpetogramma*'
- 845 col. 1, line 16: *for '*chrysippe* (F.)' read '*cydippe* (L.)'
- 848 col. 1, lines 13, 18: for 'Oenochrominae' read 'Oenochromatinae'
- 856 col. 1, line 14: *for '*Herse*' read '*Agrius*'
- col. 2, line 38: *for '*Celerio*' read '*Hyles*'; line 39, for 'C.' read 'H.'; line 41, for '(L.)' read '(Boisd.)'; line 43, for '*Ipomaea*' read '*Ipomoea*'
- 859 col. 1, line 20: for '*Scalopia*' read '*Scolopia*'
- col. 2, line 11: *for '*Ochrogaster*' read '*Teara*'; line 20, *for '*Trichetra*' read '*Trichiocercus*'
- 865 col. 1, line 4: for '*vitella*' read '*vittella*'

- 869 col. 2, lines 21–2, and wherever occurring elsewhere: for 'Platygasteridae' read 'Platygastridae'
- 875 Fig. 37.8A, B: for 'Tenthredinidae' read 'Pamphiliidae'
- 882 col. 1, line 15: *for 'Pseudagenia' read 'Fabriogenia'
- 885 under 'CLASSIFICATION', col. 3: for 'Pamphilidae' read 'Pamphiliidae'
- 900 col. 2, line 28: for 'Ctenistes' read 'Centistes'
- 903 col. 2, line 15: for 'fuscicornis' read 'fusci-cornis'
- 906 Fig. 37.22I: for 'Platygasterinae' read 'Platygastrinae'
- 907 col. 1, lines 30, 39, 50: for 'Inostemminae' read 'Inostemmatinae'; lines 28, 40, 50, for 'Platygasterinae' read 'Platygastrinae'
- col. 2, line 8: for 'Oxytelia' read 'Oxyteleia'
- 910 col. 2, lines 16–17: for 'undescribed genus' read 'Acanthobetyla'
- 913 col. 2, line 14: for 'Miomera' read 'Mio-moera'
- 917 col. 2, line 27: for 'Epientedon' read 'Epen-tedon'
- 918 col. 1, line 34: for 'Chalcodectinae' read 'Chalcedectinae'
- col. 2, penultimate line: for 'ruficornis' read 'ruficornis'
- 920 col. 1, line 26: 'Metidarnes' is a *nomen nudum*
- 923 col. 1, lines 9–10: for 'Australolelaps' read 'Australolaelaps'
- 924 col. 1, penultimate line: for 'Neoanastatus' read 'Neanastatus'
- 926 col. 1, line 29: for 'Parasclerodermus' read 'Parascleroderma'
- 929 col. 1, line 15: *for 'Pseudagenia' read 'Fabriogenia'; line 20, and elsewhere on pp. 929–31, for 'Planicepinae' read 'Epipompilus, Pompilinae-Aporini'
- 930 Fig. 37.28B: *for 'brachypterous Pepsini' read 'Iridomimus sp., Pepsinae-Pepsini'; C, *for 'Phanagenia . . .' read 'Fabriogenia sp., Pepsinae-Auplopodini'
- 935 Fig. 37.30I: for 'Zethinae' read 'Discoeliinae'
- 936 col. 2, line 2: for 'tasmaniensis' read 'humilis'; lines 41, 44, for 'Zethinae' read 'Discoeliinae'
- 937 col. 1, line 31: for 'australiensis' read 'australensis'
- 938 col. 1, line 15: for 'Priononyx' read 'Prionyx'
- 939 Fig. 37.31E: for 'Bembicinus' read 'Bembecinus'
- 940 col. 2, lines 7, 14: for 'Priononyx' read 'Prionyx'
- 941 col. 2, line 4: for 'Nysson' read 'Acanthostethus'; line 16, for 'Miscothyris' read 'Clitemnestra'; line 18, *for 'Gorytes' read 'Austrogorytes'
- 942 col. 1, lines 2, 13: for 'Bembicinus' read 'Bembecinus'
- col. 2, line 31: *for 'Diodontus' read 'Psenulus'; line 36, for 'Harpactophilus' read 'Arpactophilus'
- 943 col. 1, lines 24, 28: *for 'Notogonia' read 'Liris'
- 949 col. 2, line 43: *for 'Allodapula' read 'Braunsapis'
- 951 col. 1, line 22: *for 'Allodapula' read 'Braunsapis'
- 999 col. 3, line 52: for 'Eurylynchus' read 'Eurylychnus'
- 1010 col. 3, line 11: insert '(Bot.)' after 'Monotoca'
- 1012 col. 2, line 15: for 'Nothophagus' read 'Nothofagus'
- 1018 col. 1, lines 25–6: after 'Proctotrupes' for '904' read '905' (twice)

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